

Title	The distribution of the European sea bass, <i>Dicentrarchus labrax</i> , in Irish waters
Authors	O'Neill, Ross
Publication date	2017
Original Citation	O'Neill, R. 2017. The distribution of the European sea bass, <i>Dicentrarchus labrax</i> , in Irish waters. PhD Thesis, University College Cork.
Type of publication	Doctoral thesis
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Download date	2023-05-04 16:29:38
Item downloaded from	http://hdl.handle.net/10468/5127



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The distribution of the European sea bass, *Dicentrarchus labrax*, in Irish waters

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University College Cork, Ireland

Thesis submitted to the National University of Ireland, Cork for the degree of Doctor of
Philosophy

September, 2017

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Abstract

The European sea bass (*Dicentrarchus labrax*) can be found distributed along all coasts of Ireland in addition to most waters of the north-east Atlantic. In recent years, stocks have been declining across Europe and today there are concerns regarding the level of spawning stock biomass and the effects of consecutive years of poor recruitment. In Irish waters, comparatively little is known about the life history of the sea bass due in part to a paucity of scientific data and the cessation of the commercial fishery since 1990. On the basis of the geographical location in which sea bass were found in long term extensive offshore surveys, and the similarities of their life history trajectories in other regions, it is suggested that they represent a pre-spawning aggregation which is feeding in deeper, warmer offshore waters and is part of a larger aggregation of sea bass which extends into the Bristol Channel. These data suggest that the previously recognised Bristol Bay spawning aggregation extends westwards towards the south coast of Ireland. It is shown, based on particle tracking that it is possible for sea bass larvae to be delivered along the Irish coastline, particularly along the south coast, from both inshore and offshore putative spawning locations. This study also suggests that putative spawning locations along the south-eastern Irish coast and in offshore locations in the Celtic Sea may act as sources of larvae for localities such as south Co. Kerry which is up to 200km away, but could also contribute towards recruitment of sea bass in Northern Ireland and south-western Scotland, thus potentially impacting on sea bass recruitment regionally, nationally and internationally. The majority of acoustically tagged sea bass were detected within 0-5km from their release location only, suggesting little movement between localities and strong evidence of feeding site fidelity. Nearly a third of acoustically tagged sea bass in inshore waters were found to be resident within the area of the acoustic array for the entire period of full array deployment, including the assumed spawning season (February to June), suggesting possible spawning in inshore locations or potential evidence of the occurrence of

skipped spawning. The consecutive long absence periods for two thirds of tagged fish during this same period may suggest substantial offshore migration, which coincided with the assumed peak spawning period. The findings using pop-off satellite archival tags (PSATs), suggest that at least some sea bass that originate in both Irish and British coastal waters may aggregate in the same approximate location in the Celtic Sea during the assumed peak spawning period. Genetic information, obtained from fish sampled as part of the studies reported in this thesis, supports the contention that sea bass from inshore Irish waters, from offshore waters in the Celtic Sea and from the North Sea may be part of the same panmictic population. The evidence presented here points to sea bass occurring in Irish waters as being an integral part of the larger trans-Celtic Sea population. As a consequence, the sustainable management and conservation of the species occurring in Irish waters must be undertaken on a basis which is international, as well as local.

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Declaration

I declare that this thesis has not been previously submitted as an exercise for a degree at the National University of Ireland or any other university and I further declare that the work herein is my own, or else noted.

Ross O'Neill

Acknowledgements

Firstly, I would like to thank my supervisors Prof. Sarah Culloty, Dr Phil McGinnity and Dr Niall Ó'Maoiléidigh for their advice, guidance and encouragement throughout the course of my dissertation.

I would also like to thank my funders; the research undertaken in this project was funded by the Beaufort Grant, in addition to funding supplied by the Marine Institute. The Marine Institute also significantly aided the fieldwork for this dissertation through the provision of staff members and equipment, including offshore research vessels, to undertake the various surveys required to collect data.

The efforts of individual staff members from both UCC and the Marine Institute are also sincerely appreciated. From University College Cork, I wish to thank Dr Tom Reed for his help with the acoustic data and statistics, while from the Marine Institute I wish to thank Nigel Bond, Dr Oliver Tully, Jonathon White, Alan Drumm, Joe Cooney, Dermot Fee and Rob Bunn, among many others, without whose advice and technical abilities this study would not have been possible. A special thanks also is due Dr Mike Armstrong and Mary Brown of CEFAS for the procurement of genetic samples from the North Sea.

I would also like to acknowledge the work and expertise offered by local anglers, which greatly aided the tagging of specimens. In particular, I am extremely grateful to Dr James Barry of Inland Fisheries Ireland, Cian O'Halloran of Absolute Fishing, Sean Rooney of Bass Fishing Wexford and Jim Hendrick of ProBassFisher.

Finally, I would like to thank my family and friends for their encouragement and understanding over the past few years.

Chapter 1

The biology of European sea bass in Irish waters: a review

Abstract

The European sea bass is a long-living and slow-growing species that inhabits both inshore and offshore waters around Ireland. The species achieves sexual maturation after approximately five to seven years for females and four to six years for males and has been found to live for up to 24 years. Juveniles (<32 cm) can be found in nursery areas, typically located in the upper reaches of estuaries and creeks. After three to five years, they can be found in large shoals moving along the coastline, feeding in inshore waters during summer time. Tagging research suggests that maturing bass can be found in relatively discrete inshore locations during the summer feeding period, with research from British waters suggesting the repeated return of post-spawning adult fish to these areas annually. Results from mark-recapture research suggest that sea bass in Irish inshore waters have a high probability of being recaptured locally. Additionally, tagged adult sea bass have been recaptured in offshore waters, suggesting the occurrence of offshore migration of in adult sea bass from Irish coastal habitats. The results of previous tag/recapture programs on adult sea bass within Irish and British waters suggest that there may be a negligible movement of migrants between both countries. Additionally, genetic research also suggests the possibility of the existence of a sub-population of sea bass in Irish waters. The location of spawning areas in Irish waters is unknown however there is some suggestion that they are located inshore, in close proximity to river estuaries on the south coast. A paucity of published data and research on sea bass, in conjunction with a lack of a commercial fishery as a source of landings data, has resulted in a poor understanding of the current state of sea bass stocks within Irish waters.

Introduction

The European sea bass, *Dicentrarchus labrax* (Linnaeus, 1758), is a marine member of the perch family (Order: Perciformes, Family: Serranidae), which occupy the suborder Percoidei.

This suborder contains over 7500 species of fish distributed globally in a variety of aquatic habitats (Pickett & Pawson, 1994). The European sea bass can be found inhabiting waters stretching from the southern coast of Norway to the north-west coast of Africa and throughout the Mediterranean Sea, though it is believed that Ireland and Britain represent the major northern extent of their distribution (Pickett & Pawson, 1994; Coscia & Mariani, 2011).

Within Irish waters, only four members of the Serranidae family can be found: European sea bass (*Dicentrarchus labrax*), wreck fish (*Polyprion americanus*), dusky perch (*Epinephelus gigas*) and the comber (*Serranus cabrilla*), with the European sea bass being the most common. Historic records show that sea anglers as far back as the 19th century prized it for its tough fighting ability (Pickett & Pawson, 1994). Often visible during summer months chasing prey on the water's surface, the sea bass has long been associated with inshore waters.

Commercial exploitation of sea bass stocks in Irish and British waters began in the 1950s, though in recent years, sea bass stocks have come under sustained pressure across Europe. While it may have been assumed that the successful aquaculture of sea bass in the Mediterranean Sea could have relieved pressure on wild stocks, populations in the north-east Atlantic have continued to decline, coinciding with numerous years of poor recruitment (ICES, 2013) and an increase in fishing effort proportional to the rise in demand for the fish from consumers.

Life cycle

Sea bass are aggregate pelagic gonochoristic (separate-sex) spawners. It is necessary for males and females to release their respective gametes into the water column at the same time

due to the limited lifespan and mobility of sea bass spermatozoa (Secor, 2015). The location of spawning sites is poorly understood in Irish waters due to a paucity of commercial landings data and an absence of ichthyoplankton research. Research undertaken by Kennedy & Fitzmaurice (1968; 1972) has suggested five potential spawning locations based on the southern and eastern coasts, all of which are located within inshore waters or in the proximity of large river estuaries. These potential areas include: Waterford estuary, Youghal (Co. Cork), Splaugh Rock (Co. Wexford) and also at Dingle and Blasket Sound (Co. Kerry). The presence of spawning fish in the main sea bass angling areas, such as Dungarvan Bay and Cork Harbour, is negligible, most likely due to the possibility of spawning being limited by salinity levels (Kennedy & Fitzmaurice, 1972).

Kennedy & Fitzmaurice's (1972) findings also suggest that adult (>42cm) fish based on the south-west Irish coast do not migrate offshore to spawn, remaining in local inshore waters instead. In contrast to the absence of data on sea bass spawning in Irish waters, research based on sea bass populations in Britain has found that the majority of spawning occurs offshore during the late spring and summer months, with larvae taking between one and three months to arrive in inshore nurseries (Dando & Demir, 1985; Thompson & Harrop, 1987; Kelley, 1988; Jennings & Pawson, 1992; Coscia & Mariani, 2011).

In the Celtic Sea, migration of adult bass to spawning locations begins in late autumn and early winter, coinciding with a decrease in inshore water temperatures (Kennedy & Fitzmaurice, 1972). This decline in temperature is believed to initiate the movement of adult fish into deeper, warmer waters located offshore (Kennedy & Fitzmaurice, 1972; Coscia & Mariani, 2011), though some sea bass may remain in inshore waters (Kennedy & Fitzmaurice, 1972; Kelley, 1979). The timing of spawning events varies depending on water temperature, with sea bass populations in the Mediterranean found to commence spawning as early as December (Pawson & Pickett, 1996). In the north-east Atlantic, the spawning season

is believed to last from February through to June, with May the most important month of spawning activity in the Celtic Sea (Kennedy & Fitzmaurice, 1972; Pickett & Pawson, 1994).

The development of sexual reproduction capabilities differ between the sexes, with males achieving sexual maturation earlier in life (four to six years) than females (five to seven years) (Kennedy & Fitzmaurice, 1972; Hichem Kara, 1997; Fahy *et al.*, 2000; Pawson *et al.*, 2000; Pawson *et al.*, 2007). Males are also thought to mature earlier in the season and sustain a higher level of maturation for longer than females. Males have been observed to mature as early as November, while ripe females did not appear until late winter and early spring (Pawson & Pickett, 1996). Gonad development is assessed on a seven-point scale (Pawson & Pickett, 1996) with adolescent females found to show stage 3 development (developing) for one or more spawning seasons prior to achieving full maturation, while adult males may progress from stage 1 (immature) to stage 7 (spent) in the course of one season.

Female sea bass in Irish waters are capable of releasing between 293000 and 358000 eggs per kilo of body weight (Kennedy & Fitzmaurice, 1972). The ripening of these eggs does not occur all at once, but shedding of the eggs into the water column takes place in batches, typically over a number of weeks (Dr Mike Pawson, pers. comm.). Sea bass eggs sampled from the southern coast of Ireland were found to be between 1.20mm and 1.39mm in diameter whereas those in the Mediterranean were between 1.15mm and 1.16mm (Kennedy & Fitzmaurice, 1968). The size of the egg is believed to be related to ambient water temperatures and salinity levels, with eggs found in the cold, less saline waters of the North Atlantic being larger than those found in the Mediterranean (Wassef & Emary, 1989). It is thought that many of the eggs will succumb to hostile environmental conditions, with water temperature being a primary factor.

Water temperature is also believed to be one of the major influences affecting the location and timing of spawning events for sea bass (Pawson & Pickett, 1996), with an optimal range

between 8.5°C and 15°C thought to be required. A study by Thompson & Harrop (1987) investigated sea bass spawning sites in the English Channel and southern North Sea, finding that there was an absence of sea bass eggs in waters with an ambient temperature below 8.5°C to 9.0°C and above 15°C. Further evidence suggested that spawning locations in British waters shifted eastwards during the spawning season. In Irish waters, research carried out by Kennedy & Fitzmaurice (1968) recorded the presence of sea bass eggs at Splaugh Rock, Co. Wexford and at Youghal, Co. Cork, where water temperatures ranged from 10.5°C to 13.2°C. Survivability of the eggs may also depend on the level of predation from other marine organisms, particularly if spawning occurs in productive inshore waters where predators may be more numerous (Secor, 2015).

Upon successful fertilisation, eggs will hatch into passive drifting planktonic larvae within four to nine days, dependant on ambient water temperature (Pickett & Pawson, 1994). As larvae begin to develop, their primary food source post-hatching is a globule of low-density oil stored within the egg (Pickett & Pawson, 1994). This oil globule also provides neutral buoyancy which keeps the larvae afloat within the water column. Once the globule is absorbed, sea bass larvae begin feeding on a mixture of phytoplankton and small zooplankton.

Research under laboratory conditions has found that sea bass larvae are ‘cruise predators’, with movement behaviours showing continuous and intense swimming which increases significantly with development, particularly 10 to 20 days post-hatching (Georgalas *et al.*, 2007). However, at the time of hatching, sea bass larvae are between 4.0mm and 4.5mm long and therefore possess little mobility. This results in the direction of their transport being determined by oceanographic physical processes such as tidal currents, prevailing winds and wave action. While spawning may occur in approximately the same region every year, the contemporary weather conditions at the spawning location may significantly influence the potential dispersal of the sea bass larvae. The movement behaviour used by sea bass larvae

during the larval transport phase has not been observed in the wild, while there is also uncertainty about whether sea bass larvae actively swim towards nursery locations or are opportunistically and passively transported into them (Kennedy & Fitzmaurice, 1972). Their behaviour may be similar to the larval phases of other marine fish which have been found to exhibit diel vertical migration (DVM) behaviour, moving through the water column in response to fluctuations in luminosity levels (Grave, 1981; Clark & Levy, 1988; Haldorson *et al.*, 1993; Auditore *et al.*, 1994).

Nursery habitats offer protection from hostile weather conditions which exist within the open ocean, but may be susceptible to variations in temperature and salinity over short time periods (Martinho *et al.*, 2009). The surface geography and associated algal and epifaunal communities also allow for evasion from predators during the first few years of sea bass development (Aprahamian & Barr, 1985). Certain man-made structures and activities may create artificial nurseries for juvenile and developing sea bass, including those located in the vicinity of power station warm-water outflows (Pawson & Eaton, 1999). The warm water emitted at these locations allows for an increased rate of metabolism, meaning increased growth rates, particularly by alleviating the decrease in growth during the colder winter and spring months (Pawson & Eaton, 1999). At approximately 2cm long, the fry become recognisable macroscopically as juvenile bass. The nursery area becomes home to the juvenile for the next three to four years as they develop into adolescents (32–42 cm) (Fig. 1.1).

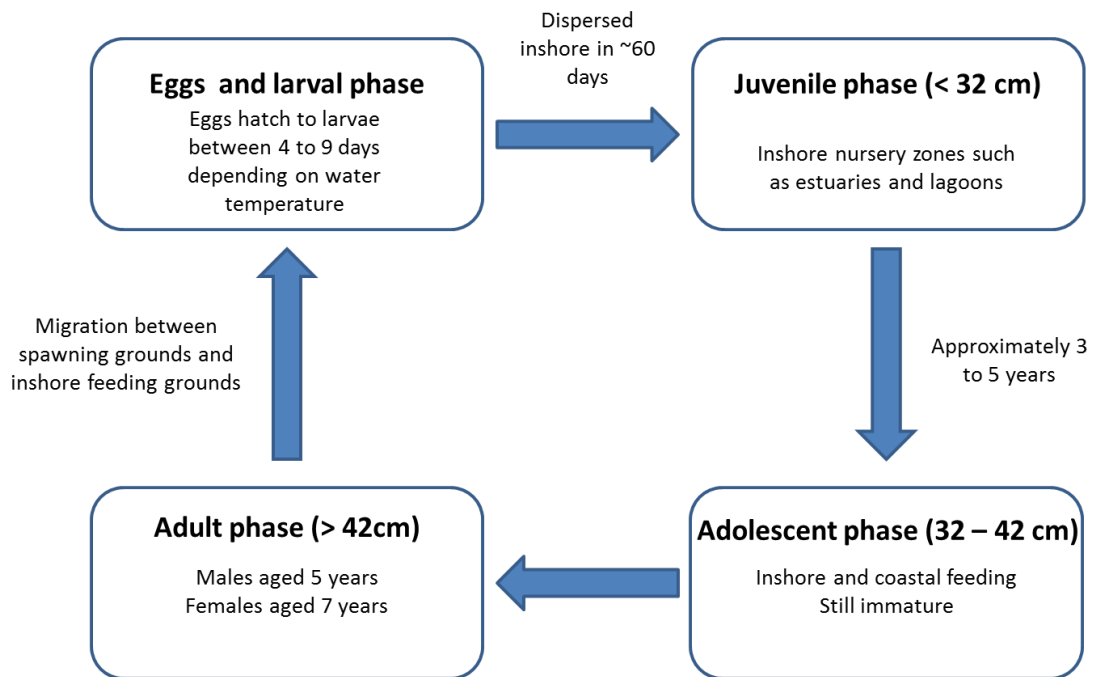


Fig. 1.1 The four primary phases of the sea bass life cycle (from Pawson et al., 1987; Pickett & Pawson, 1994; Pawson et al., 2007)

Adolescent sea bass form shoals and move out of the nursery zones to feed in inshore coastal waters. Sea bass at this size are colloquially known as ‘schoolies’ due to their schooling behaviour. They can typically be found in shoals in inshore waters, though they can also migrate over considerable distances (up to 500km) along the coast (Pawson *et al.*, 1987). Some adolescent sea bass display evidence of partial gonad maturation, particularly during late summer and early autumn, though the vast majority are not thought to be sexually mature enough to spawn (Pickett & Pawson, 1994; Pawson *et al.*, 1996).

Female sea bass measuring over 42cm are considered to be adults, while males over 35cm can also be considered capable of sexual reproduction. While a number of females measuring 29-30cm have been observed at stage III maturity (early developing), this was only recorded in a small number of fish while several specimens of males <36cm having been recorded at maturity stages IV (late developing) through VII (spent) (Pawson & Pickett, 1996). This length is attained typically after five years in males and up to seven years in females in the

waters of the north-east Atlantic (Pickett & Pawson, 1994). Sexually mature adults migrate annually between relatively discrete inshore feeding areas and spawning grounds, where they release their gametes into the water column during the assumed spawning season between February and June.

Unfavourable and harsh climatic and environmental conditions impact significantly on recruitment to the stock with juvenile sea bass mortality in shallow estuarine nursery areas particularly vulnerable to fluctuations in freshwater input and water temperature. Cold winters between 2008 and 2012 were believed to have been responsible for the decline in recruitment in this period (ICES, 2014). In contrast, favourable conditions, such as warm summers and mild winters, can lead to the development of strong year classes and a resulting increase in recruitment in the proceeding period (Holden & Williams, 1974; Kelley, 1979; ICES, 2014).

Anatomy

The morphology of the sea bass has evolved to suit the varied marine environments in which it inhabits. The colour of the fish is optimised to allow for stealth when foraging for prey, while also camouflaging against potential predators. The colouration on the dorsal/flanks of the fish differs depending on the type of environment it inhabits. Sea bass which frequent areas such as reefs and kelp beds typically have darker dorsal flanks to allow them to blend in with their environment and are therefore known colloquially as ‘black jacks’. Meanwhile, sea bass living over sand or gravel substrate have a lighter silver colour and may be known as ‘sand bass’ (Pickett & Pawson, 1994). Colouration on the ventrum of the fish tends to be white, providing shading against the sky when observed from below. This form of colouration is known as countershading (Ruxton *et al.*, 2004) and confers protection to the sea bass from predators hunting above and below.

Physical protection from predators is in the form of spines which can be found in both the main dorsal fin and on the operculum (gill cover). Sea bass scales are also relatively large, with adult scales possessing a radius of between 4mm and 8mm (ICES, 2015), and offer protection to the fish from the abrasive nature of high-energy habitats, such as storm beaches and rocky shores. Scales can also be used to determine age and growth rates as each year concentric rings, known as annuli, are added. The wider, lighter-coloured bands represent summer feeding, when growth rates are at their highest, while the thin, dark rings represent the colder waters of winter and early spring, which result in reduced metabolism (Ostrander, 2000).

Sea bass movement is achieved through subcarangiform locomotion, with swimming ability originating from the alternation of contracting muscles on both sides of the rear half of the fish. This form of locomotion results in reduced manoeuvrability compared to other motion types, such as anguilliform, but allows for rapid acceleration and the ability to sustain high swimming speeds. Previous observations on sea bass swimming ability has found that juvenile/adolescent fish, measuring 24cm to 32cm, are able to hold station in currents up to 80cm/s^{-1} , while others have reported sea bass present in waters where mean flow rates were 200cm/s^{-1} (Pickett & Pawson, 1994). This rapid increase in acceleration can be used when escaping predators and also when foraging for prey. The ability to sustain a high average swimming speed is also evident from the results of tag/recapture studies, with sea bass having been found to travel at a mean speed of 26.6km/day^{-1} over 18 days (Kelley, 1979).

Development of sea bass can result in morphological changes to their appearance. While juvenile sea bass may have a more pointed head, this becomes more rounded as they mature into adults. Males and females grow at similar rates until approximately five years old, which is around the time of sexual maturation, at which point females have been found to grow at significantly faster rates than males (Pawson & Pickett, 1996). Females have also been found to live longer than males (Kelley, 1979).

Habitat

Though sea bass spend their lives in the marine environment, they are euryhaline fish capable of tolerating low levels of salinity and can often be found at the upper tidal limits of estuaries (Dando & Demir, 1985; Pickett & Pawson, 1994; Dufour *et al.*, 2009). In Irish inshore waters, Kennedy & Fitzmaurice (1972) recorded the presence of bass 18 miles up the Waterford estuary at 18 PSU (Practical Salinity Unit) while Fahy *et al.* (2000) found juveniles in locations with salinities varying between 17 PSU and 21 PSU. This ability to transition into brackish waters allows for access to additional prey sources, protection from predators and areas of shelter which are not available to other fully marine species.

Sea bass can often be found in close proximity to underwater structures and along rocky coastlines, where inshore reefs and trenches offer shelter and refuge, as well as access to potential prey. Sea bass are also occasionally present in the waters of surf beaches, particularly after periods of stormy weather, feeding on epifaunal and infaunal prey which become dislodged through hydraulic wave action (Pickett & Pawson, 1994). Estuarine zones also offer shelter and, due to their high productivity, may provide more varied and abundant sources of prey, resulting in year-round usage by sea bass.

Sea bass larvae migrate into nursery habitats in river estuaries, salt marches and lagoons approximately 30 to 90 days post-spawning (Kelley, 1988; Jennings & Pawson, 1992; Pickett & Pawson, 1994). These well-sheltered areas serve as nurseries to the post-larval fry (which are less than a year old) and older juvenile fish (<32cm) as they develop. The low salinities found within the shallow nursery habitats can accelerate the growth rate and development of the post-larval sea bass, believed to be due to energy saving from reduced osmoregulation and easier swimming conditions (Salliant *et al.*, 2002; Dando & Demir, 1985). Distribution and abundance of juvenile sea bass less than a year old (termed 0-group) within these nurseries may be limited by river run-off, precipitation levels and wind direction (Martinho *et*

al., 2009), while the distribution of prey species within the nursery zone is also believed to influence juvenile bass presence (Kennedy & Fitzmaurice, 1972). Adolescent sea bass (32-42cm) are predominately found in shoals in inshore coastal waters, with tag/recapture results from British waters finding that 56% of all adolescents were recaptured within 80km of their release location. However, some of adolescent sea bass were recorded crossing open bodies of water, with one fish recaptured on the German coast over 500km from its original tagging location (Pawson *et al.*, 1987).

Adult sea bass (>42cm) can be found inhabiting inshore locations between late spring and autumn, where they forage for prey. There is some evidence to suggest that adult sea bass will disperse from areas of high disturbance, such as marinas or areas of fishing pressure, while larger, older fish, typically females, can often be found travelling solo or in pairs (Pickett & Pawson, 1994). During late winter and early spring, adult sea bass are believed to undertake reproductive-driven migrations to offshore waters, returning to the same relatively discrete inshore areas annually between these migrations (Kelley, 1979; Pawson *et al.*, 1987; Pawson *et al.*, 2008). While the length of time adult sea bass spend in offshore waters is unknown, there is some evidence to suggest that there may be a proportion of the sea bass population that are nomadic, constantly migrating between inshore and offshore locations. Pickett & Pawson (1994) noted migratory shoals of ‘golden bass’ which appeared off Plymouth in 1983, distinct to the south-east coast of England, which have subsequently appeared in large shoals on both sides of the English Channel.

Diet

During the larval stage, the primary source of nutrients for a sea bass is from the yolk of its egg, sustaining the larvae for up to the first 72 hours of its life (Klaoudatos *et al.*, 1990) and eventually being absorbed over the next nine to 25 days (Pickett & Pawson, 1994). The

larvae then progresses on to exogenous food sources in the form of zooplankton such as rotifers (*Branchionus* spp.) and brine shrimp nauplii (*Artemia* spp.) (Pickett & Pawson, 1994). Nursery zones provide 0-group bass with a varied diet consisting of copepods, gammarids, mysids and small gastropods, among others (Kennedy & Fitzmaurice, 1972; Aprahamian & Barr, 1985; Kelley, 1987).

As juvenile bass (<32cm) develop into adolescents (32-42cm), their diet begins to vary. Other prey species, such as smaller common shore crabs (*Carcinus maenus*), various prawn and shrimp species, marine worms (*Arenicola* spp., *Nereididae* spp.) and small fish fry, are targeted by adolescent fish (Kelley, 1987). While progressing to adulthood, the percentage of crustacean and fish in their diet further increases, with larger fish consuming fewer prey items but of larger size (Kelley, 1987). Sea bass caught in offshore locations are almost exclusively piscivorous. Targeted commercial fisheries for Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*) or horse mackerel (*Trachurus trachurus*) often report catching sea bass which are believed to be feeding on the pelagic shoals (Pickett & Pawson, 1994). Larger fish found in inshore waters may consume grey mullet (*Mugil cephalus*), sandeels (*Ammodytes* spp.) and a variety of small flatfish species, in addition to a range of various molluscs and crustaceans (Kelley, 1987). The large buccal cavity of an adult sea bass mouth enables it to consume large prey (up to 335mm), as well as a significant volume of prey (Spitz *et al.*, 2013)

Sea bass are opportunistic feeders, able to switch prey species depending on the geographical location and the time of year. They are also adept at taking advantage of prevailing weather conditions and physical features to feed. While sandy surf beaches may appear devoid of foraging opportunities when exposed at low tide, storm conditions can disturb the sediment, releasing epifaunal and infaunal benthic invertebrates and other animals into the water column offering a variety of foraging opportunities for sea bass within the locality. Sea bass can also often be present in areas of strong tidal flow, such as locations of constriction in

estuarine channels, where they can remain stationary in the lee of holes or divots on the channel bed, out of the effects of the main currents (Kennedy & Fitzmaurice, 1972). By remaining out of these currents, sea bass can easily hold position and forage on prey which is carried by the ebbing or flooding tides, while conserving energy. Colder water temperatures reduce metabolic activity and feeding levels in sea bass (Kelley, 1987), evident in the high levels of vacuity observed in bass in the months of January, February and March (Pickett & Pawson, 1994).

Migration and stock interconnectivity

Adult sea bass are capable of travelling over large distances in relatively short time periods, as revealed by previous tag/recapture studies undertaken using basic identification tags in British (Holden & Williams, 1974; Pawson *et al.*, 1987; Fritsch *et al.*, 2007; Pawson *et al.*, 2007; Pawson *et al.*, 2008) and Irish (Kennedy & Fitzmaurice, 1972) waters. Evidence from these studies suggests that when in inshore waters, movement of sea bass is primarily localised (Pawson *et al.*, 1987). Juvenile movements are typically restricted to the nursery zone in which they are found and are influenced by environmental conditions (Kelley, 1988; Martinho *et al.*, 2009). The majority of adolescent sea bass remain within approximately 80km of their nursery zone, but some have been reported to travel considerable distances across open water (Pawson *et al.*, 1987). While adult fish may exhibit a more discreet selection of inshore summer feeding locations than adolescent shoals, the extent of migration range and movement is believed to expand with increasing fish size and age, particularly concerning winter migrations to pre-spawning feeding areas and to spawning locations (Holden & Williams, 1974; Pawson *et al.*, 1987).

The repeated presence of adult sea bass at relatively discrete inshore locations on an annual basis suggests the possibility of the use of homing ability by sea bass in returning to their nursery zones (Pawson *et al.*, 2008). Sea bass tagged with simple identification markers in Irish inshore waters has also revealed short-range movement patterns along the coastline (Kennedy & Fitzmaurice, 1972). For example, fish tagged in the Dungarvan Bay area were later recaptured further to the east along the coast, with some entering the Waterford estuary approximately 36 miles away. The period of absence recorded between release of tagged fish and recapture was between zero and 364 days, with increasing periods of absence not related to an increase in distance from release location. Holden & Williams (1974) recorded an absence period of 1066 days for one tagged specimen in British waters. While the majority of recaptures of tagged fish within Irish waters have been local (<50km), there is also evidence of long-range movements recorded in Irish waters. In one instance, a fish tagged off the south-west coast in inshore waters was recaptured three weeks later, 60km offshore of the south-east coast (Pawson *et al.*, 2007). The absence of a targeted commercial fishery within Irish waters has resulted in a scarcity of data, particularly regarding offshore stocks (Fahy *et al.*, 2000) and may account for the perceived localisation of stocks within Irish inshore waters (Holden & Williams, 1974; Pawson *et al.*, 1987).

Tagging studies undertaken on sea bass in the English Channel, Bay of Biscay and southern North Sea (Holden & Williams, 1974; Pawson *et al.*, 1987; Fritsch *et al.*, 2007; Pawson *et al.*, 2007; Pawson *et al.*, 2008) have revealed annual migration routes for adult bass within British coastal and offshore waters. It is believed that sexually maturing fish originating along the western coast of Britain will migrate south during winter to join up with aggregations of fish originating from the Cornish and Devonshire coast in the eastern Celtic Sea and Bristol Channel (Pawson & Pickett, 1996). Fish from the southern coastline of Britain are believed to move west towards the western English Channel and Bay of Biscay. Fish tagged on the Welsh coast at Anglesey were found to travel over 800km south to

spawning grounds off the Cornish peninsula (Kelley, 1979; Pawson *et al.*, 1987), while another specimen was reported by Pawson *et al.* (2007) to have travelled from the Channel Islands to the south of the Bay of Biscay (a minimum distance of 1200km) in less than two months. Populations of bass on the southern British coastline migrate over much shorter distances than those on the eastern or western coastlines, suggesting that the centre for bass distribution is based in the waters along the southern British coast (Holden & Williams, 1974; Pawson *et al.*, 1987). Kennedy & Fitzmaurice (1972) also suggested that the highest abundances of sea bass in Irish waters were to be found on the southern coastline between Wexford and Kerry. The apparent centralisation of sea bass populations in both Ireland and Britain may be due to the increase in temperature changes in inshore waters at higher latitudes, which experience a larger increase in cooling between late autumn and early spring.

With the exception of a single fish documented by Pawson *et al.* (2007), there has been no other reported recapture of tagged sea bass originating from Irish or British waters in either's respective inshore waters. Fahy *et al.* (2000), however, suggested that the offshore spawning aggregations formed in the Celtic Sea may be an amalgamation of stocks from both Irish waters and British waters. The findings of Coscia & Mariani (2011) suggest that, at a level of 13 microsatellite loci, sea bass populations in southern Ireland and western Britain are genetically similar. However, a previous genetic analysis of sea bass from four separate regions (Bay of Biscay, English Channel, Scotland and Ireland) has suggested the potential existence of a separate population in Irish waters, while at the same time confirming links between sea bass populations in the English Channel and the Bay of Biscay (Fritsch *et al.*, 2007). While tagging returns from fish tagged in Irish and French studies suggest that the rate of emigration (fish recaptured outside the waters of the country in which it was tagged) of sea bass is negligible (Holden & Williams, 1974), offshore pelagic spawning by sea bass may limit genetic differences between populations in the waters of north-west Europe, with larvae and eggs being dispersed over a wide area post-release (Jennings & Pawson, 1992).

Management of sea bass in Irish waters

The commercial exploitation of sea bass stocks in Irish waters began primarily in inshore waters in the 1950s. The dominant method of fishing was the use of handlines, rod and line and monofilament nets (Fahy, 1981). Often bycatch from the commercial fishery for grey mullet, landings of sea bass began to grow as the fish increased in popularity. The fishery was almost exclusively inshore and catches were seasonal, with the highest landings recorded from May to October, averaging 92 tonnes annually for this period between 1963 and 1976 (Fahy, 1981). Analysis of catch data, however, revealed that landings were declining from the time that statistical information of the fishery became available. This decline in the sea bass populations became particularly evident throughout the 1970s and culminated in the introduction of the Bass (Conservation of Stocks) Order in 1990 and the closure of the commercial fishery, partially as a result of overexploitation in conjunction with years of poor recruitment (IFI, 2014). Since then, any data regarding sea bass stocks in Irish waters has come as a by-product of other scientific studies, surveys and angling reports (Fahy *et al.*, 2000; IFI, 2014; Marine Institute, 2015). Though the current state of the stock profile is unknown, it is thought to be significantly depleted and not yet recovered from the historic low levels of the late 1980s. Both the International Council for the Exploration of the Sea (ICES) (2012) and the findings of the tag/recapture study by Pawson *et al.* (2007) consider sea bass stocks in Irish waters discrete in comparison to other areas from a management perspective.

Currently, no Irish registered vessel is permitted to fish for, transport or possess any sea bass on board in EU territorial waters, while there is also a complete ban on fishing for sea bass within the Irish 12-mile limit for all nations. A source of frustration to Irish commercial fishermen, however, is that vessels registered in other EU states such as France and Belgium and also Britain are allowed to target and retain sea bass outside the Irish 12-mile limit, while Irish vessels are forced to discard catches. The recreational fishery for sea bass is highly

popular in Irish waters, having gained notoriety among foreign anglers for larger-sized specimens. The retention of sea bass as a result of angling may be substantial, particularly in Britain and France (Pawson *et al.*, 1987), though catch and release is common in Irish waters. Management of sea bass stocks in Irish waters is the responsibility of Inland Fisheries Ireland (IFI) and the Sea Fisheries Protection Authority (SFPA), who monitor commercial landings and fishing activity. Prior to 2016, a bag limit of two fish per angler per 24-hour period was enforced in Ireland, with fish required to be over 40cm long. In addition, there was a closed season from May 15th to June 15th, whereby no angling for bass is permitted (IFI, 2014). These protective controls were replaced at beginning of 2016 by emergency measures introduced by the European Commission and enforced in the Celtic Sea, Irish Sea, English Channel and North Sea. Implementations of these measures were due to concerns over declining stocks of sea bass in within these waters. The legislation prohibited the retention of sea bass by both commercial fishers and anglers from January 1st to June 30th. For the period between July 1st and December 31st, anglers are allowed to retain a maximum of one fish per day with a minimum size limit of 42cm, as per Council Regulation 559 (EC, 2016). Commercial fishing can also operate in this period in E.U. waters, outside the Irish inshore zone, though pair-pelagic trawling is still prohibited (ICES, 2016).

Catches of sea bass in offshore waters (>12nm from the coastline) indicate the presence of the species in open, deep waters. Anglers fishing in British waters often encounter sea bass when fishing over sunken wrecks in the English Channel, though this occurrence is extremely rare in Irish waters, with most sea bass being caught from angling boats taken around reefs and sandbars. The negligible level of commercial sea bass fishing by other European fishing fleets in offshore Irish waters is believed to be due to low stock densities, though on occasion, significant catches have been recorded in offshore waters off the southern coastline (Kennedy & Fitzmaurice, 1972; Pawson *et al.*, 1987). Prior to the cessation of this practice

during the first six months of 2016, the majority of offshore commercial sea bass fishing took place in the English Channel, Bay of Biscay and southern North Sea (ICES, 2012; 2014).

As previously mentioned, one genetic study and a number of tag/recapture programs have suggested that there may be negligible interaction, and therefore gene flow, between sea bass originating in Irish waters and those from other regions. If this is the case, given the assumed low stock level which resulted in the closure of the fishery in 1990, the lack of recruitment input from outside sources may significantly hinder or delay the recovery of populations in Irish waters. It is also possible that the Irish population may be self-recruiting, which would suggest that it may be a significant period of time before the population has achieved sustainable levels.

Objectives

The life history of the bass is complex and poorly understood in Irish waters. Though a substantial amount of research has been undertaken on the species in British and French waters, the status of sea bass populations in Irish waters is uncertain, with little targeted research having been undertaken since the early 1970s. There is, in particular, an absence of information relating to where sea bass of Irish origin spawn and the inter-relatedness between fish found inshore and those occurring at offshore locations. The method by which sea bass larvae are transported to coastal nursery zones from these spawning areas is also poorly understood.

While previous data from tag/recapture studies suggests negligible interaction between Irish sea bass and those originating from other regions within European waters (such as the North Sea, Bristol Channel, western British coast and Bay of Biscay) advancements in tag technology in recent years, particularly with the advent of acoustic and satellite tracking, may

allow for more informative studies. Additionally, while previous genetic studies disagree as to the existence of a distinct Irish sea bass population, there is potential for a more thorough investigation, using a larger sample size and focusing specifically on sea bass found in inshore Irish waters and offshore spawning aggregations within the Celtic Sea.

Therefore, the objectives of this study were:

1. To undertake a study of the biology and distribution of sea bass occurring in offshore waters around the coast of Ireland using data collected from the Irish GroundFish Survey (IGFS). There is a paucity of information regarding the biology of sea bass in offshore Irish waters, particularly in relation to assumed offshore migration during late autumn and early winter period. Our primary aim was to explain the observed geographical distribution of catches through analysis of the historic catch data, available from 2003 to 2015, provided by the annual survey undertaken during late autumn and early winter by the Marine Institute. Analysis of data collected on these surveys of aspects of sea bass biology was also undertaken to establish a picture of general biological characteristics and structure of the populations encountered and screened; length/weight relationship, retrospective growth rates, conditioning factor, sexual maturity distribution and year classes for years where data were available. These results are presented in Chapter 2.
2. To investigate potential sea bass larval dispersal from putative spawning sites in Irish coastal and offshore waters in a particle tracking model. Real-time tracking of fish larvae in the wild is unfeasible with particle tracking models offering a theoretical simulation of the potential dispersal of larvae in relation to various environmental influences. The model outputs provided an indication as to the potential larval transport pathways to the Irish coast and an estimation of the possible extent of recruitment into Irish coastal nursery zones from both inshore and offshore spawning

scenarios. The results of the model output and implications of the findings are discussed in Chapter 3.

3. To use acoustic telemetry to examine the use of inshore habitats by adult fish over a 12 month period, including the assumed spawning season of February to June. Previous research based in British waters has suggested that adult sea bass make annual offshore migrations to spawn. However, in contrast, limited studies undertaken in Irish waters have suggested the possibility that sea bass spawn in inshore waters. The presence of sea bass within coastal habitats on the southern Irish coast was investigated using acoustic tags, which provided an indication as to fish residency within inshore waters during this spawning period. The influence of environmental factors, such as diurnal and tidal cycles, on sea bass behaviour was also analysed. The results of this investigation are presented in Chapter 4.
4. To use pop-off satellite archival tags (PSATs) to potentially identify offshore spawning locations, migratory routes to spawning locations and fidelity to inshore feeding locations for sea bass tagged in Irish waters. Previous evidence, though limited, has suggested that sea bass of Irish origin can be found in offshore waters in the Celtic Sea. These locations have been previously identified as areas where sea bass of British origin spawn. Identification of offshore spawning locations for sea bass of Irish origins will allow for a better understanding concerning larval dispersal and inter-relatedness with sea bass from other regions such as the western coast of Britain. Therefore, in Chapter 5, the results of data obtained from sea bass tagged with PSATs both from inshore Irish waters and offshore in the Celtic Sea are discussed. The movements of tagged fish over time and in relation to ambient water temperatures were examined while the findings were also analysed in relation to evidence of inshore site fidelity

5. To further the understanding of whether the sea bass population in Irish waters is genetically distinct. Limited previous studies have shown that sea bass populations in north-west Europe exhibit little variation in stock structure, though some suggestions have been made that the population in Irish waters may be genetically distinct. Microsatellite analysis was undertaken on samples of coastal fish in Irish waters and offshore in the Celtic Sea. These findings are discussed in Appendix 4.0. The findings of this investigation will provide an insight into the validity of the existence of a sub-population of sea bass within Irish waters while also examining the possibility of a panmictic stock within the Celtic Sea and surrounding marine environs.
6. To provide advice concerning the potential future research and management plans regarding European sea bass. The overall implications of the findings from this thesis are discussed in Chapter 6.

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Chapter 2

A study of the biology of the European sea bass (*Dicentrarchus labrax*) caught in offshore locations in the Celtic Sea

Abstract

A survey of ground fish was carried out at approximately 162 locations around the Irish coast on an annual basis from late October to December as part of the Irish GroundFish Survey (IGFS). Biological data provided by catches of sea bass (*Dicentrarchus labrax*) on the IGFS provide a unique opportunity to determine the species spawning distribution in Irish coastal waters and to acquire novel life history information. Using data collected on 693 sea bass caught between 2003 and 2015, it can be observed that in November, within the constraints of the area sampled by the IGFS, maturing sea bass are aggregating almost exclusively at a single location in the Celtic Sea, in an area between the south-east coast of Ireland and the approaches to the Bristol Channel. It is important to note that, apart from a very few locations along the south coast and in the Irish Sea, sea bass do not occur in substantial densities offshore anywhere else around the Irish coast. The possible explanation of the observed distribution may be due to a combination of the spawning and growth benefits associated with the ambient water temperature in the Celtic Sea in addition to prey availability in offshore waters.

Captured fish were found to have a mean length of 52.9cm; both males and females are maturing sexually, generally at the same rate (stage 4); fish are typically 8.7 years of age, though the oldest fish encountered was an 18 year old female caught in 2006; males and females are approximately the same age; the ratio of males to females varies among years, with either sex dominating in a given year. While there is inter-annual variation in these life history parameters, there does not appear to be a temporal trend. Evidence from recent surveys also suggests that most of the sea bass have been feeding shortly before capture. The observed life history values are similar to those reported for sea bass captured in waters off the west coast of Britain. On the basis of the geographical location in which these fish are found and the similarities of their life history trajectories, it is suggested that they represent a pre-spawning aggregation which is feeding in deeper, warmer offshore waters and is part of a

larger aggregation of sea bass which extends into the Bristol Channel. These data suggest that the previously recognised Bristol Bay spawning aggregation extends westwards towards the south coast of Ireland.

Introduction

Previous studies (Kennedy & Fitzmaurice, 1972; Fahy *et al.*, 2000) provided a glimpse into the movements and behaviour of the sea bass, *Dicentrarchus labrax*, in Irish waters, concluding that sea bass stocks in Irish waters were essentially local, though the absence of a regulated and large-scale commercial fishery probably enhanced this perception (Holden & Williams, 1974). Since these studies, and due in part to an absence of commercial landing data, there has been an absence of scientific information regarding stock structure, fish movement and population levels in this species. As a result of a sustained period of poor recruitment across Europe (ICES, 2016a) and declining stocks, there is renewed interest in understanding the biology of the species, particularly in regions which are data deficient, such as around the coast of Ireland. Sea bass in Irish waters are mostly associated with inshore locations, predominately on the southern coastline, though shoals are occasionally encountered in offshore waters (>12 nautical miles from the coast) (Kennedy & Fitzmaurice, 1972; Marine Institute, 2012; Marine Institute, 2015). Juveniles (<32cm) remain within inshore nursery zones, such as lagoons, backwaters and estuaries, prior to their classification as adolescents (32-42cm) at the age of approximately three to six, when they form shoals, moving along the coast foraging for prey (Kennedy & Fitzmaurice, 1972; Kelley, 1979; Picket & Pawson, 1994). Adult fish (>42cm) feed in summer and autumn periods in relatively discrete inshore locations and often return annually to the same areas post-spawning (Pawson *et al.*, 2008).

The migration of sexually mature adult fish to spawning locations coincides with declining water temperatures at the end of autumn and beginning of winter (Pawson & Pickett, 1987). Offshore spawning locations have been identified in the English Channel, Bristol Channel and southern North Sea where the majority of spawning is believed to occur (Thompson & Harrop, 1987; Pickett & Pawson, 1994), while it is suggested that inshore spawning takes place in Irish waters, particularly on the southern coast (Kennedy & Fitzmaurice, 1972). In the Celtic Sea, spawning aggregations may be comprised of shoals of fish from different regions, using the same migratory route (Kelley, 1979; Fahy *et al.*, 2000). Sea bass spawning is pelagic, with the location of spawning sites varying on an annual basis dependant on regional fluctuations in water temperatures. It is believed that a lower water temperature threshold of 8.5 to 9°C is necessary for larval survival and for the commencement of spawning activity (Thompson & Harrop, 1987; Pickett & Pawson, 1994; Pawson *et al.*, 2007).

While data from commercial sea bass fisheries in British waters allows for the assessment of population dynamics and changes in biological trends, no such information is available regarding Irish populations due to the closure of the commercial fishery in 1990 (Marine Institute, 2015). The Marine Institute conducts an annual survey, the Irish GroundFish Survey (IGFS), of commercial fishing grounds around the Irish coast. The aim of this survey is to investigate the status of contemporary stocks of demersal fish within Irish waters through standardisation of average catch per defined haul, which can then be used as an indicator of species abundance (Stefánsson, 1996). Occasional catches of sea bass have been recorded on these surveys, with data available for catches between 2003 and 2015.

The aim of this study is to investigate the biology of the sea bass captured at offshore locations during the annual IGFS. Here an analysis of morphometric differences, growth rate, conditioning, age profile, sexual maturity, gonadosomatic index and feeding levels of sea bass caught between 2003 and 2015 are presented and, where possible, compared with

previously published data to investigate the changes in biological parameters over this period and to explore the hypotheses that sea bass in Irish waters are different to those found in other regions in Europe. Explanations for the observed distribution of sea bass from survey data are also offered.

Materials and methods

Sampling locations

The coastal waters of Ireland are sampled annually to estimate the abundance and distribution of ground fish, particularly commercially important gadoid species. Waters of the north-east Atlantic Ocean and Celtic Sea coasts are surveyed by the Marine Institute, while the Agri-Food and Biosciences Institute (AFBI) of Northern Ireland are responsible for organising surveys in the Irish Sea. Stations typically sampled by both authorities are displayed in Fig. 2.1. Between 2005 and 2011, the IGFS sampled between 138 (2005) and 176 (2010) stations annually (mean = 162; SD = 11) between late October and early December, depending on weather conditions. A total of 349 unique stations were fished between 2005 and 2011. The Northern Irish GroundFish Survey (NIGFS) typically samples 62 stations in the Irish Sea annually.

IGFS stations were fished during daylight hours to ensure standardisation of results. At each survey station a 30 minute trawl along the sea floor was conducted. The sampling gear used on the IGFS was the French Grand Overture Verticale (GOV) net, designed to target species feeding on and above the seabed. The codend lining consisted of 400 stretched meshes of 20mm each, giving a total length of 8m. The total circumference of the lining was 600 meshes (ICES, 2012). The trawl headline height was provided by net sensors and measured 4.5m with speed maintained at approximately four knots for the duration of the tow. The net

spread was achieved through the use of Morgere FP 10 trawl doors mounted on either side of the net. Sensors were fitted to the net and trawl equipment to ensure that the net fished correctly (Marine Institute, 2012). Once caught, fish were sorted by hand for analysis.

Biological data recorded

The data recorded for sea bass on IGFS varied depending on survey protocol in a given year and is displayed in Table 2.1.

Table 2.1 Available biological data recorded by the Marine Institute from sea bass catches between 2003 and 2015

Year	No. of fish	TL (cm)	Weight (g)	Sex	Maturity	Age	Retrospective growth calculations
2003	1	Yes					
2004	13	Yes					
2005	6	Yes					
2006	85	Yes	Yes	Yes		Yes	
2007	36	Yes	Yes	Yes		Yes	
2008	3	Yes	Yes	Yes	Yes		
2009	23	Yes	Yes	Yes	Yes		
2010	24	Yes	Yes	Yes	Yes		
2011	32	Yes	Yes	Yes	Yes		
2012	7	Yes	Yes	Yes	Yes		
2013	25	Yes	Yes	Yes	Yes		
2014	370	Yes	Yes	Yes	Yes	Yes	Yes
2015	69	Yes	Yes	Yes	Yes	Yes	Yes

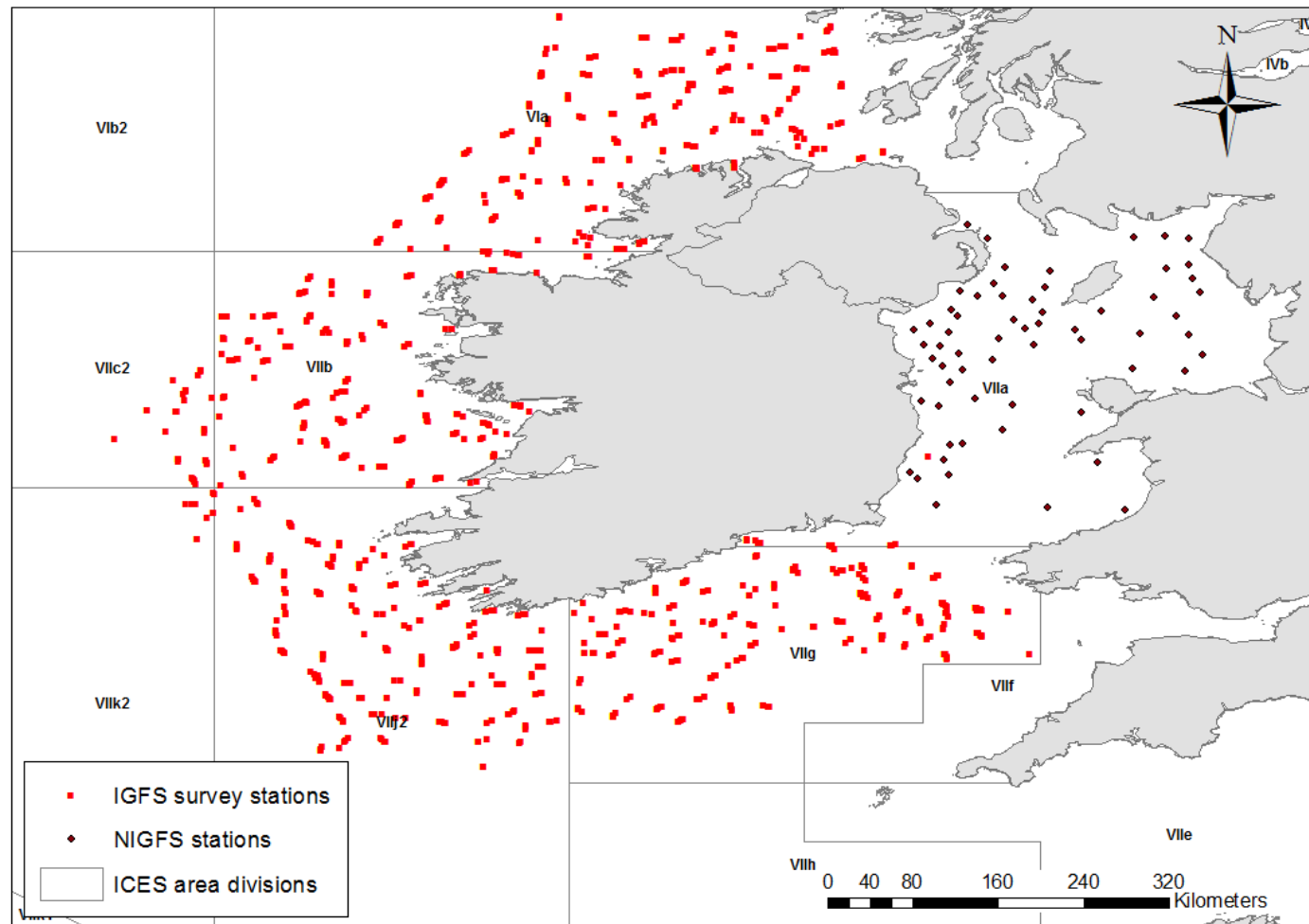


Fig. 2.1 All IGFS stations (red - 2003 to 2015) and NIGFS stations (black – 2009 to 2012) stations sampled to assess stocks of commercially important ground fish, such as gadoids, in Irish waters

Fish length

For surveys undertaken between 2003 and 2015, catch location and length data for all specimens were recorded. The total length (TL) of the fish was defined as the length of the fish measured from its most anterior point to its most posterior point, in this case being the extent of the compressed tail (Fishbase, 2016), and this was recorded for all specimens. All lengths were measured to the nearest 0.5cm. Total length (TL) was the parameter used throughout the rest of this study.

Condition indices

Where length and weight data were available, condition index for specimens were calculated using Fulton's condition factor, K , based on the following equation as per Htun-Han (1978):

$$K = \frac{W \times 100}{L^3}$$

where W is the fish weight in grams and L is the total length of the fish in centimetres.

Growth rate and ageing

Retrospective growth rate calculations were recorded for scales obtained from specimens caught on IGFS 2014 and 2015. Scales were taken from behind the pectoral fin on sampled fish, as this area is less likely to have damaged or replaced scales. The solution for cleaning scales was prepared by mixing a teaspoon of sodium peroxide (Na_2O_2) with 300ml of water until dissolved. Where sufficient samples were available, three scales per fish were placed into individual glass scale wells and 5ml of the solution added via pipette, with the scale wells labelled for identification. Scales were left for up to one hour before being extracted via

tweezers. Remaining organic matter was removed using tissue paper and the scales were then rinsed in freshwater and patted dry. A gelatine based solution ($\frac{1}{4}$ teaspoon gelatine dissolved in a 5cm x 2.5cm tube with some hot water until a slight reduction in viscosity is observed) was pipetted on to a labelled microscope slide and the dried scales carefully placed on top using a mounting needle. Care was taken to ensure no air bubbles were trapped under the scales which may have affected their readability. Slides were readable after approximately 30 minutes.

The method of back calculation of length at age was based on distances between annuli was developed by Lea (1910) and was adopted by Pickett and Pawson (1994) for use on European sea bass scales. The equation adopted is:

$$L_n = \frac{R_n}{R} L$$

where L_n is the length of the fish at year of age n , R_n is the distance of annuli n from the nucleus, R is the total radius of the scale and L is the fork length of the fish at the time of capture. Annuli distances were recorded using an internal measure in the microscope eyepiece.

Age results were available for subsamples of fish from the following years: 2006 ($n = 29$), 2007 ($n = 26$), 2014 ($n = 50$) and 2015 ($n = 30$), while all specimens from the 2009, 2010 and 2011 surveys were aged. Two specimens from the 2007 survey and two from the 2014 survey were unable to be aged due to damaged scale samples. Cross-checking by another scientist of aged scales was undertaken for samples from 2006, 2007, 2009, 2010 and 2011.

Sex, maturity and gonadosomatic index (GSI)

Sex and maturity were identified and categorised based on a 7-point scale adopted from Pickett and Pawson (1994) (Appendix 1.1). In some cases, fish sex was not recorded or identified (n = 151). A change in the sampling protocol for IGFS 2015 enabled specimens to be retained for analysis post-survey and therefore gonad weights were available. A gonadosomatic index (GSI) was used to calculate the sexual maturity of an animal based on comparative relative mass (%) of the gonads to the overall (somatic) mass of the fish (Pickett & Pawson, 1994). The GSI was calculated using:

$$GSI = \frac{Gw}{Sw} \times 100$$

where Gw was the weight of the gonad and Sw was the somatic weight of the fish (ungutted weight).

Stomach contents and vacuity

Additional stomach content data were available for fish from the 2015 IGFS. Where possible, stomach contents (namely macroscopically identifiable partially digested or undigested whole fish) were identified at species level identification keys on board the *RV Celtic Explorer*. No analysis of smaller gut contents (undigested bones, etc...) was undertaken, but their presence was recorded.

Results

Catch locations

Out of a total of 349 different survey locations sampled by the IGFS between 2003 and 2015, sea bass were encountered at a total of 51 survey stations at 36 unique locations, with some locations recording multiple catches over different years of surveys (Fig. 2.2). In the NIGFS, sea bass were captured at eight locations out of the 62 stations fished between 2009 and 2012, though biological data from fish caught on NIGFS are not used in this study. Of the 693 sea bass recorded on the IGFS from 2003 to 2015, 690 (99.4%) were recorded from ICES division VIIg, with the remainder caught in VIIa ($n = 1$) and VIIj ($n = 3$). All fish were caught in the 25 day period from November 6th to December 1st across all surveys.

Sea bass were caught at depths of between 41.9m and 114.5m, with a mean depth of 79.8m ($SD = 12.9$ m) over all of the surveys. The average number of catch locations for sea bass per survey was 3.92 ($SD = 1.81$). Sea bass were caught at six separate sampling stations in 2006 and 2013, while surveys in 2003, 2004 and 2005 recorded sea bass presence at only one sampling station for each year. Modelled mean sea surface temperature (SST) data, provided by the Marine Institute (Marine Institute, 2016), varied at sea bass catch locations annually from 2012 to 2015 (Fig 2.3). The highest mean SST was recorded in 2014 ($n = 4$) at 14.03°C ($SD = 0.31$), followed by 2015 ($n=2$) at 13.6°C ($SD = 0.2$). SST was found to be 13.14°C ($SD = 0.27$) at sea bass stations in 2013 ($n=5$) and the lowest recorded value was found in 2012 ($n=5$) at 12.64°C ($SD = 0.28$).

Length/weight results

The size range and catch size of sea bass caught from 2003 to 2015 varied considerably (Table 2.2), with the largest size range of fish recorded in 2006 (38-82cm, n=85). Analysis of the distribution of length frequencies found that the majority of all fish sampled were in the 49-51.1cm range (Fig. 2.4). Discounting the 2003 and 2008 catch (n = 1), the smallest mean length observed for all fish was in 2004 at 49cm (SD = 3.7). Significant differences were found in mean fish lengths over survey years (ANOVA; $p < 0.001$). Results of the Tukey HSD found that mean fish length from the 2006 survey were highly significantly larger ($p < 0.001$) than those of the 2007, 2009, 2013, 2014 and 2015 surveys and significantly larger than those of 2011 ($p < 0.05$) (Fig. 2.5).

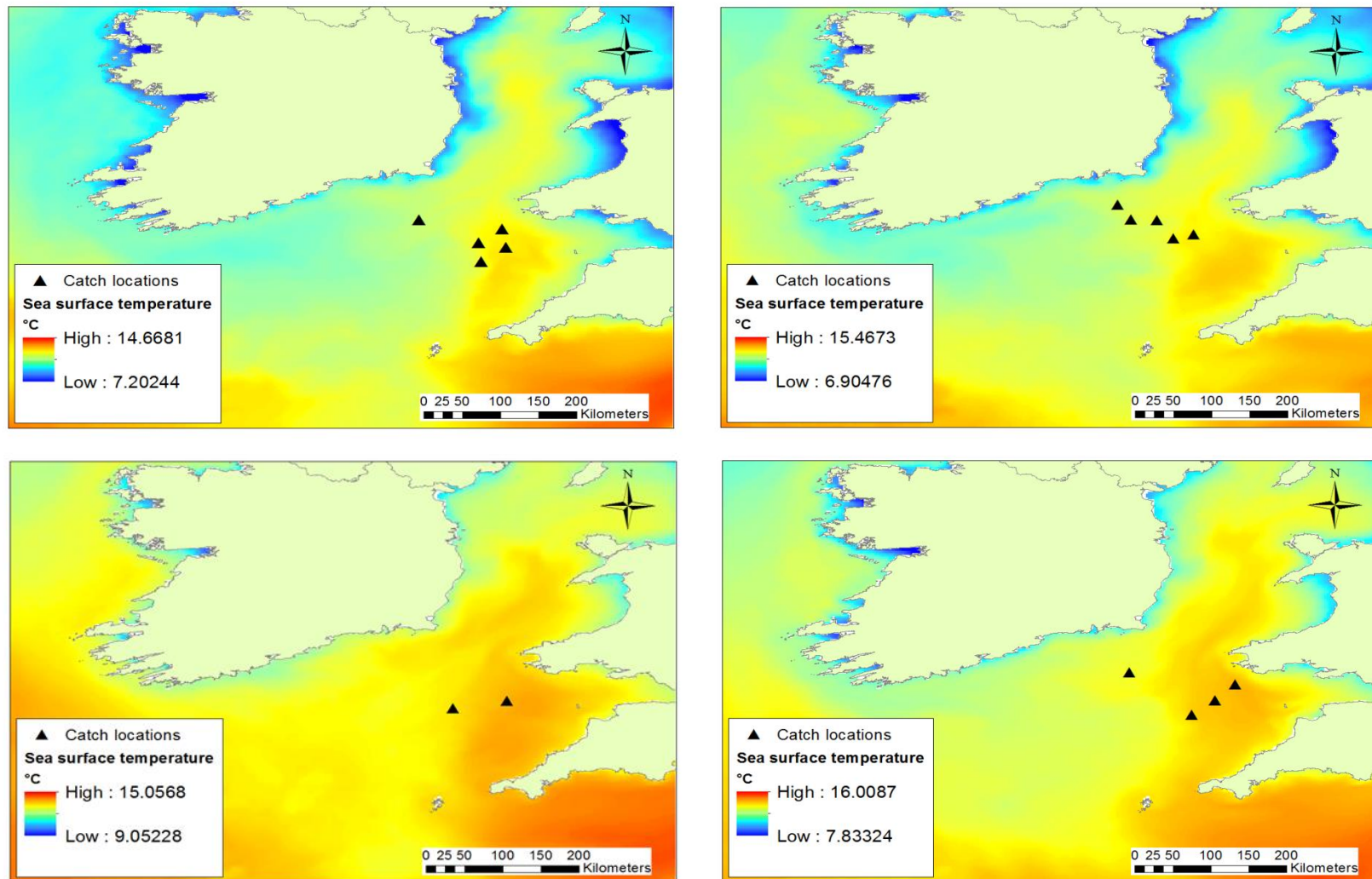


Fig. 2.3 Locations of sea bass stations and modelled mean sea surface temperatures for November 2012, 2013, 2014 and 2015 (Marine Institute, 2016) with the respective IGF surveys (clockwise from top left) shows evidence of correlation between sea bass presence and warmer SST in the Celtic Sea

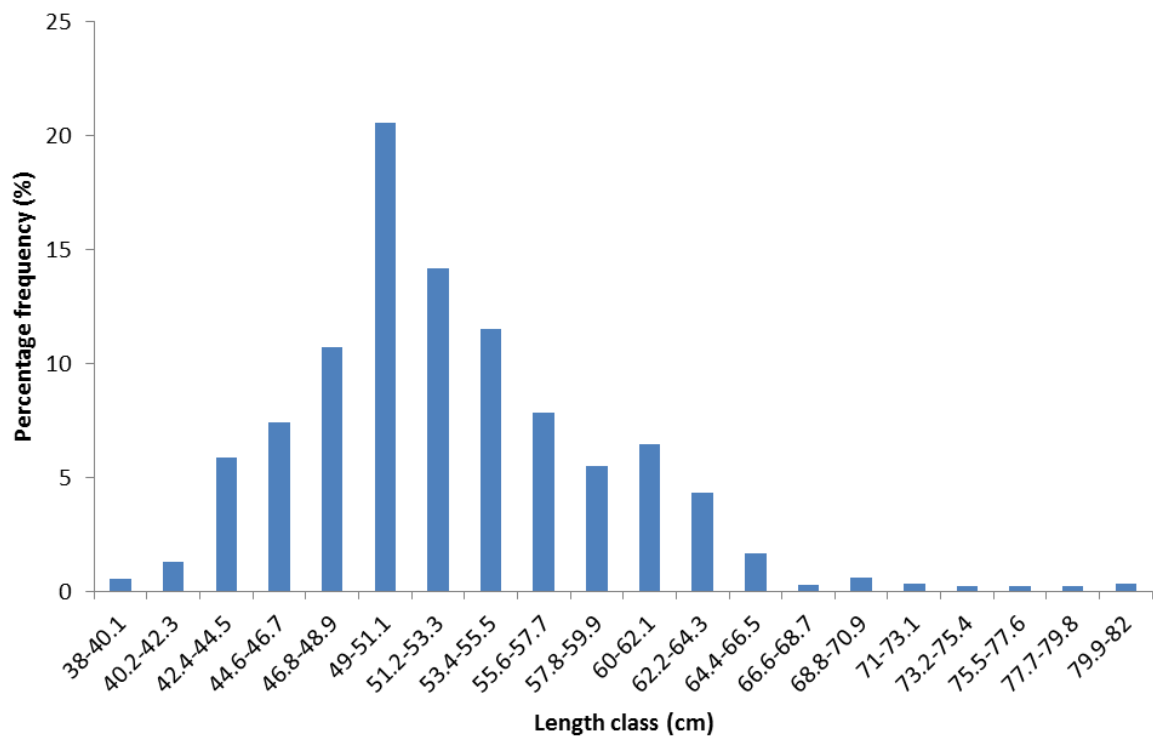


Fig. 2.4 Percentage frequency (%) of all sea bass specimens recorded on IGFS surveys from 2004-2007 and 2009-2015 (fish from 2003 and 2008 surveys excluded due to low sample sizes)

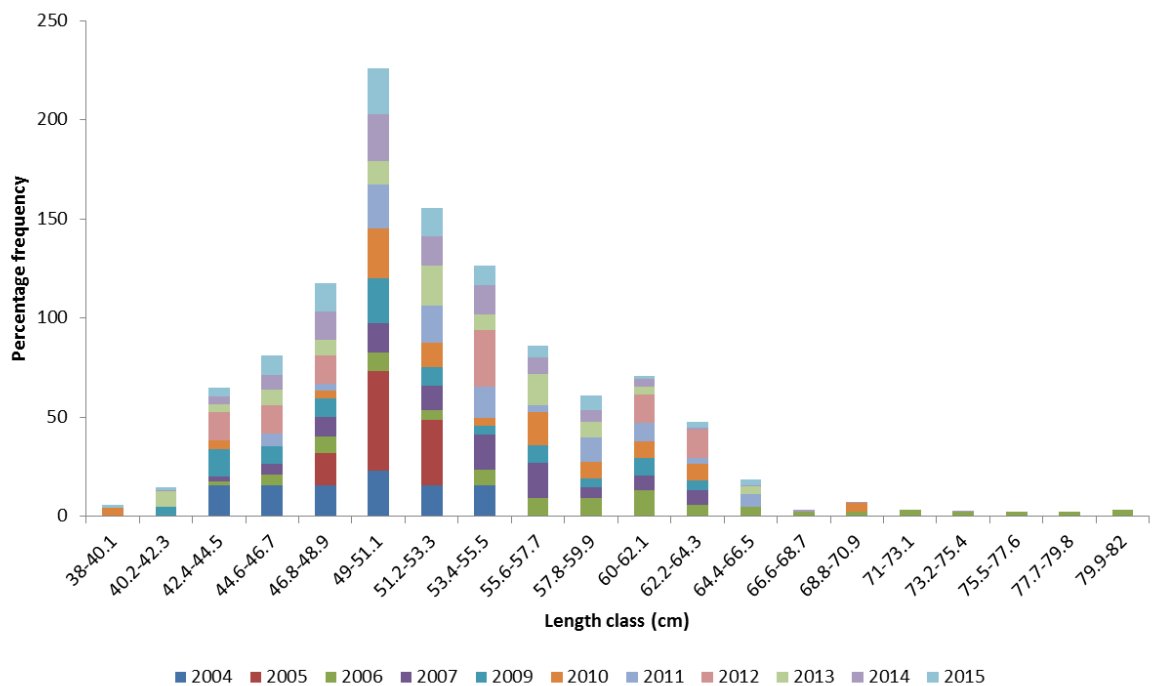


Fig. 2.5 Percentage frequency (%) by year of sea bass specimens recorded on IGFS surveys from 2004-2007 and 2009-2015 (fish from 2003 and 2008 surveys excluded due to low sample sizes)

The largest mean male length was recorded on the 2011 survey at 54.7cm (SD = 5.4) and the smallest on the 2009 survey at 46.7cm (SD = 3.3) (Fig. 2.6). Females from 2010 had the largest mean length (54.4cm, SD = 6.8), while those from 2013 were the smallest (50.2cm, SD = 7.3).

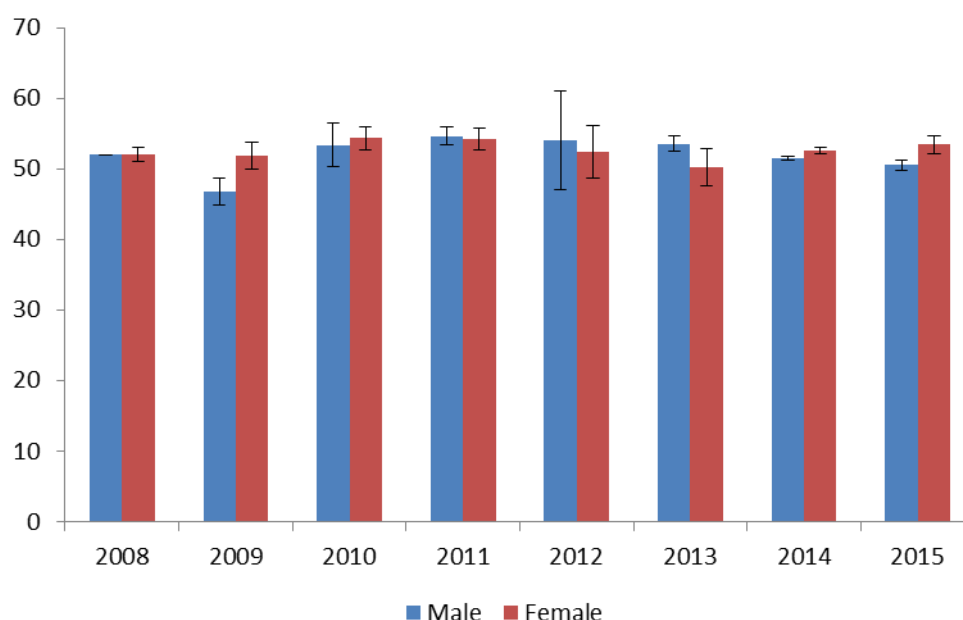


Fig. 2.6 Change in mean fish length (\pm standard error) by sex from 2008 to 2015 showed annual variations in lengths of both males and females

There was no significant difference between male and female lengths in fish caught on IGFS 2009 to 2014, though males from IGFS 2015 were significantly larger than females (ANOVA; $p < 0.05$). Analysis of the length/weight relationship resulted in a mean relationship (R^2) value of 0.859 for all fish (Fig. 2.7). The effect of sex on fish weight was found to be highly significant, with females found weigh more than males (ANOVA; $p > 0.001$). The total catch of sea bass from IGFS 2014 had a mass of 617.1kg, which represented 0.02% of the ICES recommended total allowable catch (TAC) for that year.

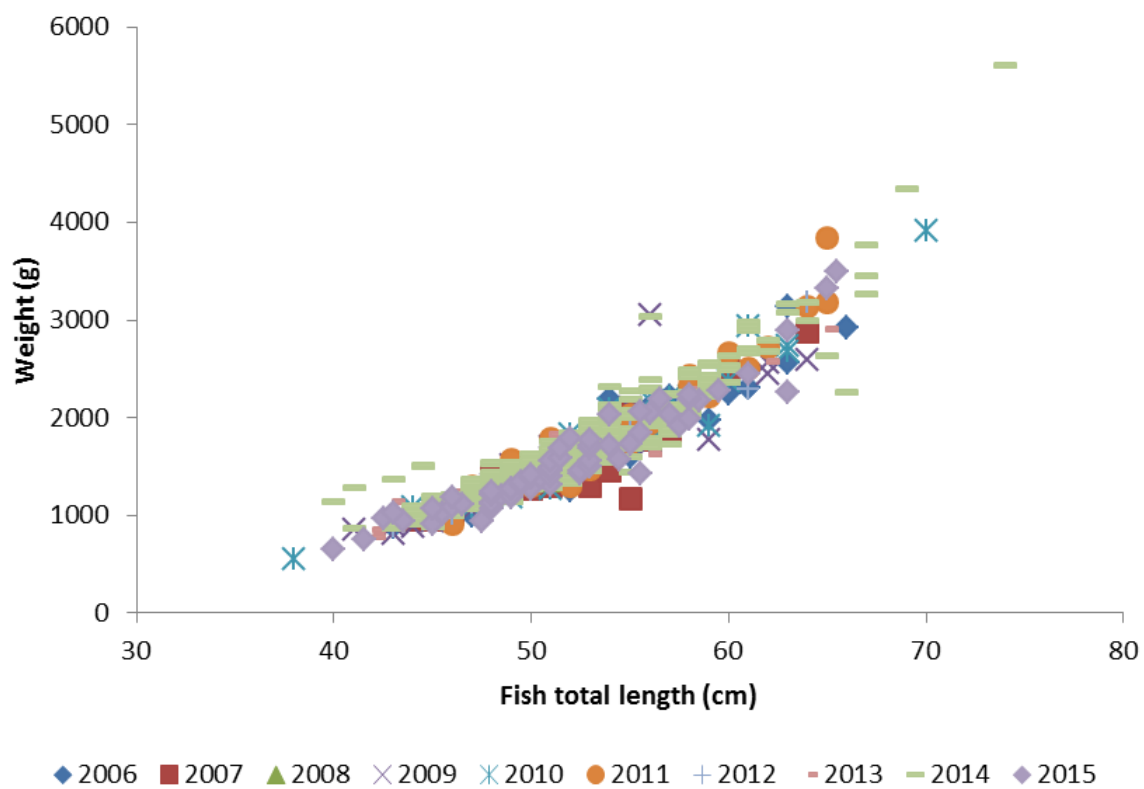


Fig. 2.7 Length/weight relationship for all fish from IGFS 2006 to 2015 (n = 607)

Table 2.2 Summary of biological data recorded for 2003-2015 IGF surveys. Numbers in parentheses “()” denote standard deviation

	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	Total
No. of fish	1	13	6	85	36	3	22	24	32	7	25	370	69	693
Unsexed-U, Male-M, Female-F	U-1	U-13	U-6	U-85	U-36	M-1, F-2,	M-4, F-15, U-3	M-5, F-19	M-20, F-12	M-2, F-5	M-16, F-9	M-201, F-162, U-7	M-24, F-45	M-294, F-248, U-151
Size range (cm)	44	43-55	48-53	43-82	44-64	51-53	41-64	38-70	45-65	43-64	42-65	40-74	40-65.5	38-82
Mean length all fish (cm)	44 (0)	49 (3.7)	50.5 (1.7)	58.8 (9.6)	53.5 (5.2)	52 (1)	51.2 (6.5)	54.2 (6.7)	54.5 (5.3)	52.8 (7.3)	52.4 (5.8)	51.9 (5.0)	51.5 (5.4)	52.9 (6.4)
Mean length male (cm)						52 (0)	46.7 (3.3)	53.4 (6.2)	54.7 (5.4)	54 (7.0)	53.6 (4.3)	51.5 (4.3)	50.5 (4.8)	51.7 (4.6)
Mean length female (cm)						52 (1.5)	51.8 (7.1)	54.4 (6.8)	54.3 (5.1)	52.4 (7.4)	50.2 (7.3)	52.6 (5.6)	53.5 (5.9)	52.7 (5.9)
Mean weight (g)				1710.3	1537.3	1510	1592	1849.7	1917.5	1779.4	1669	1667.8	1549.9	1669
Mean male weight (g)						1583 (0)	1217.3 (327.5)	1713.6 (558.1)	1943.6 (595)	1712 (579)	1721 (401.8)	1579.6 (395.2)	1414.2 (401.3)	1585 (435.7)
Mean female weight (g)						1473.5 (122.5)	1606.5 (580.1)	1885.5 (619.6)	1874.7 (743.9)	1806.4 (825.8)	1575.4 (622.2)	1781.8 (650.1)	1804.3 (667)	1773.1 (667.5)
Total fish length/weight R ² value				0.902	0.821	0.789	0.811	0.906	0.896	0.952	0.922	0.847	0.897	0.859
Mean K (all fish)				1.082 (0.1)	1.069 (0.11)	1.072 (0.04)	1.094 (0.1)	1.108 (0.1)	1.144 (0.11)	1.13 (0.08)	1.13 (0.1)	1.155 (0.09)	1.092 (0.09)	1.108 (0.09)
Mean K male						1.12 (0)	1.16 (0.09)	1.10 (0.1)	1.16 (0.09)	1.05 (0.04)	1.10 (0.07)	1.135 (0.09)	1.072 (0.08)	1.12 (0.09)
Mean K female						1.045 (0.03)	1.077 (0.1)	1.11 (0.11)	1.12 (0.13)	1.16 (0.08)	1.19 (0.13)	1.18 (0.09)	1.13 (0.1)	1.16 (0.1)
Percentage ratio male:female (n)						33:67	21:79	21:79	62:38	22:78	64:36	55:45	65:35	54:46
Most abundant male maturity (stage range)						4 (4)	3 (2-4)	3 (3)	3 (3-5)	No dominant (2-3)	4 (3-6)	4 (3-6)	4 (2-6)	4 (2-6)
Most abundant female maturity (stage range)						4 (4)	3 (3-4)	3 (3-4)	4 (3-5)	3 (2-4)	5 (2-6)	4 (2-5)	4 (2-5)	4 (2-6)
Mean age				9.1 (2.3)	9.3 (2.4)		7.8 (2.6)	8.9 (2)	8.9 (1.9)			8.8 (2.1)	8.1 (1.4)	8.7 (2.1)
Mean male age							7.5	8.8	9.4			9.1	8.1	8.8
Mean female age							7.8	9	8.1			8.3	8.1	8.3
Most abundant year class				1997	1999		2003	2002	2003			2007	2006	2003
Most abundant male year class							No dominant	No dominant	2002			2005	2006	2003
Most abundant female year class							2002	2002	2003			2007	2006	2002

Condition results

Fish condition differed significantly over survey years (ANOVA: $p < 0.001$), with Tukey HSD results finding that fish from IGFS 2015 were in significantly ($p < 0.001$) better condition than those from IGFS 2014. Overall, males were found to have a significantly poorer condition compared to females (ANOVA; $p < 0.001$) (Appendix 1.2). There was no significant relationship observed between condition index values and age or among year classes, though the relationship between maturity and condition index was found to be significant (ANOVA; $p < 0.05$), with stage 5 fish having significantly better condition than stage 4 (Tukey HSD; $p < 0.05$).

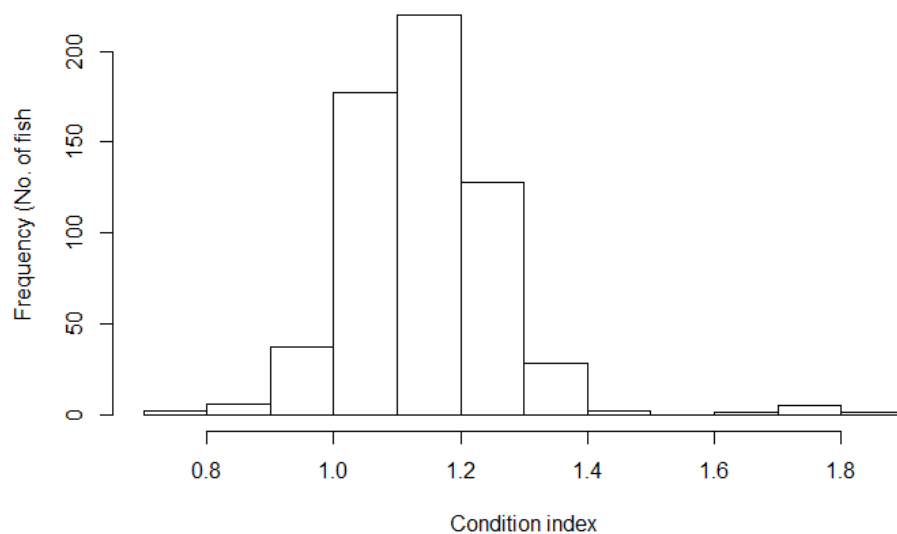


Fig. 2.8 Frequency distribution of condition indices (K) for fish from IGFS 2003 to 2015 where data were available ($n = 607$) showed that the majority of fish had a K value of between 1.0 and 1.2 (mean = 1.14, SD = 0.1)

Growth rate and ageing results

Females were found to have a higher mean growth rate over their lifespan (5.49cm/yr^{-1} , SD = 0.73) than males (5.07cm/yr^{-1} , SD = 0.65) ($p < 0.05$). No significant difference was observed

for mean growth rates for all fish from 0 to five years of age across all year classes. In addition, there were no differences observed between male and female growth from age 0 to five years (Welch test; $p>0.05$), but growth rates for fish from both IGFS 2014 and 2015 showed that in fish aged six years or older, females grew at significantly faster rates than males (Welch test; $p<0.05$) (Fig. 2.9). No significant difference in final year estimated mean length increases for both males and females from IGFS 2014 and 2015 were observed (ANOVA, $p>0.05$).

The oldest fish sampled was an 18 year old female caught in 2006. The annual mean age of the fish sampled ranged from 7.8 years in 2009 to 9.3 years in 2007. Overall, the majority of fish were found to be aged between 7 and 9 years (Fig. 2.10). There was no significant difference in the mean age of the fish over the time series (ANOVA; $p>0.05$). A significant effect on age, controlling for length and weight, was found with males older than females (ANCOVA, $p<0.05$).

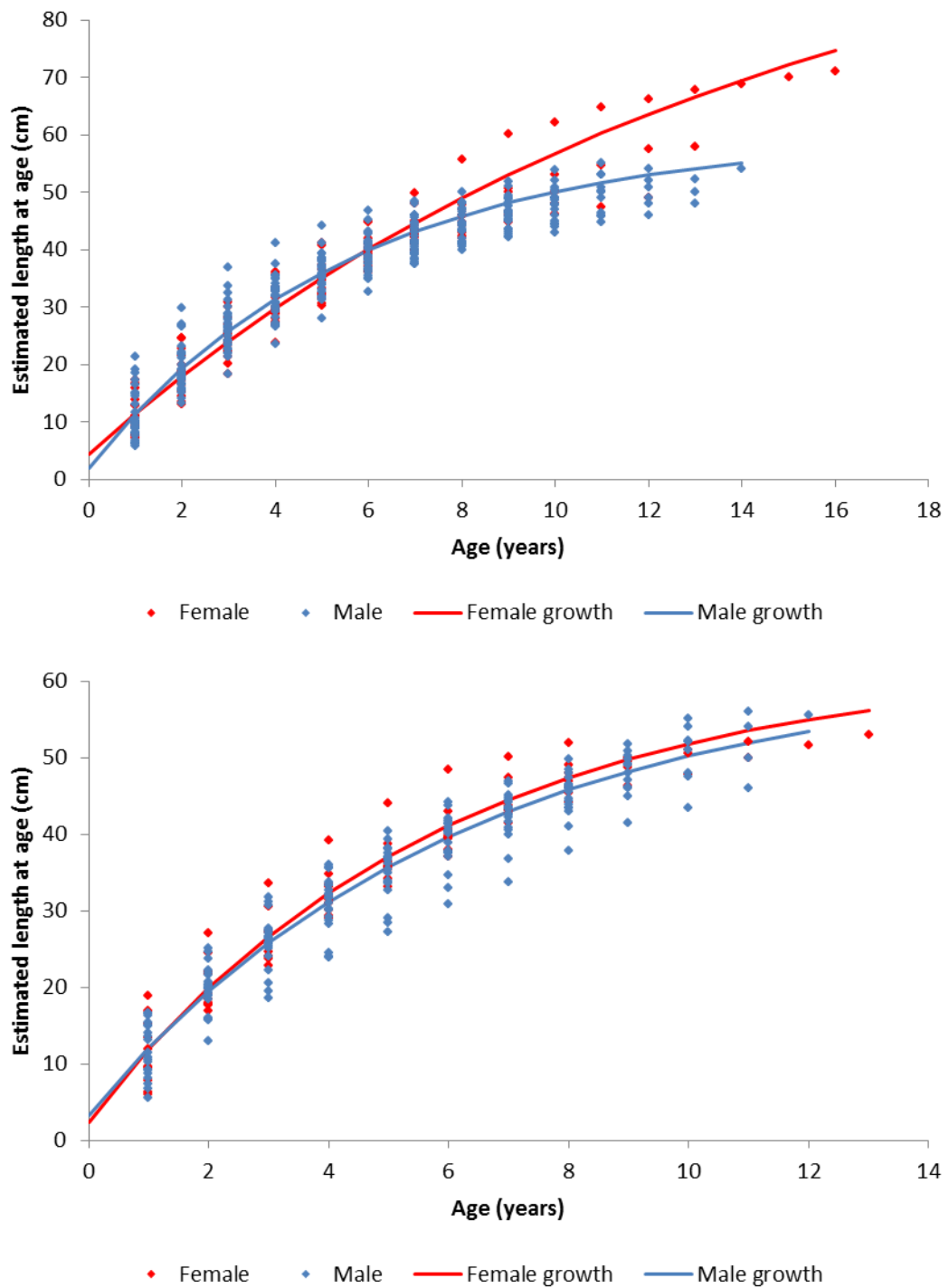


Fig. 2.9 Estimated mean length at age of aged male and female specimens (with respective von Bertalanffy growth curves) for IGFS 2014 (top)(males = 31, females = 19) and IGFS 2015 (bottom)(males = 20, females = 10) found that females grew significantly faster than males from age six onwards

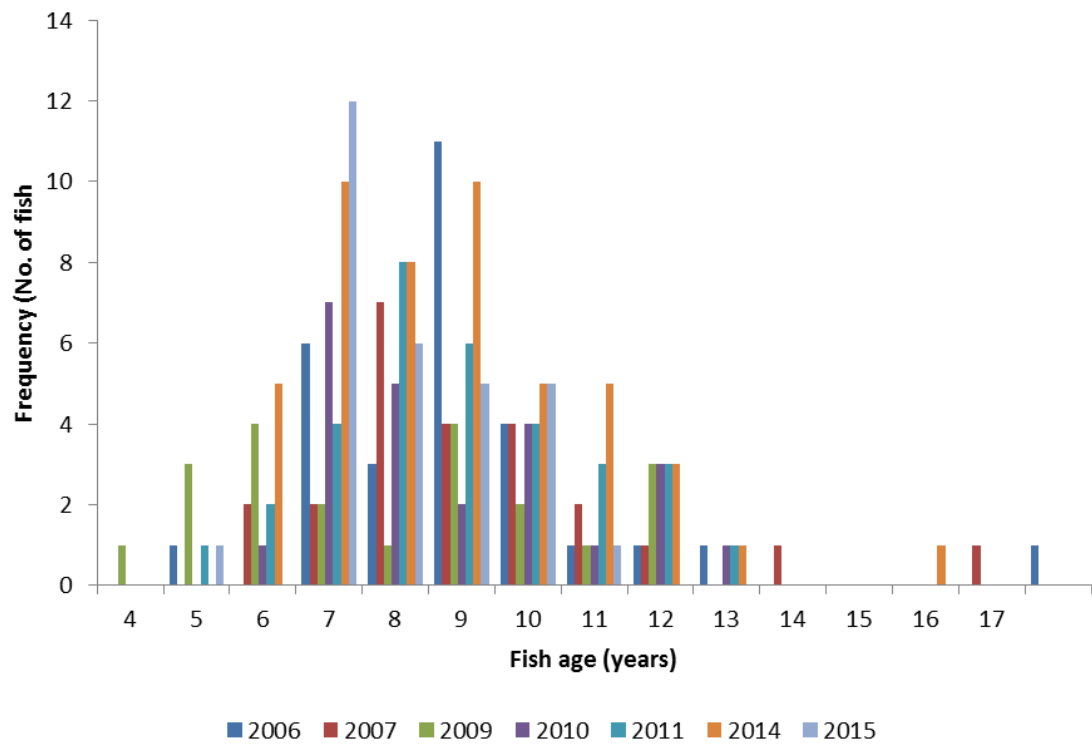


Fig. 2.10 Analysis of frequency distribution of fish age over the survey years of 2006, 2007, 2009, 2010, 2011, 2014 and 2015 found no significant differences in age composition over different survey years with the majority (59%, n = 123 of 208) of fish aged between 7 to 10 years

A number of different year class periods were strongly represented (Table 2.3). The 2006 and 2007 samples were found to be dominated by the 1997 (representing 37% of total catch that year) and 1999 (representing 29% of total catch that year) spawning cohorts respectively. There was also noticeable representation from the 2002 and 2003 spawning year cohorts in the surveys carried out in 2009, 2010 and 2011. IGFS 2014 specimens showed strong representation from 2005, 2006 and 2007 cohorts, while among the fish captured in IGFS 2015, there was a prevalence of fish spawned in 2006, which represented 40% of the sampled fish from that survey. The strong year classes from the mid-1990s through to the early 2000s documented by ICES (ICES, 2013) are evident in the reported catches here.

Table 2.3 Number of fish per year class of aged specimens from samples taken on 2006, 2007, 2009, 2010, 2011, 2014 and 2015 IGF surveys

Year class ⇒	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2
Survey year	9	9	9	9	9	9	9	9	9	9	9	9	0	0	0	0	0	0	0	0	0	0
	8	8	9	9	9	9	9	9	9	9	9	9	0	0	0	0	0	0	0	0	0	0
	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
2006	1				1	1	1	4	11	3	6		1									
2007		1			1		1	2	4	4	7	2	2									
2009								2		1	2	4	1	3	5	2	1					
2010								1	3	1	4	2	5	7	1							
2011										1	3	3	4	6	8	4	3					
2014										1				4	5	5	10	8	10	5		
2015															1	6	5	6	12		1	

Sex, maturity and gonadosomatic index (GSI) results

The ratio of males to females was higher in four surveys (2011, 2013, 2014 and 2015) where data for sexed fish were available (Fig. 2.9). Overall, slightly more of the specimens collected over the entire duration of the surveys were males (54.1%, n=294).

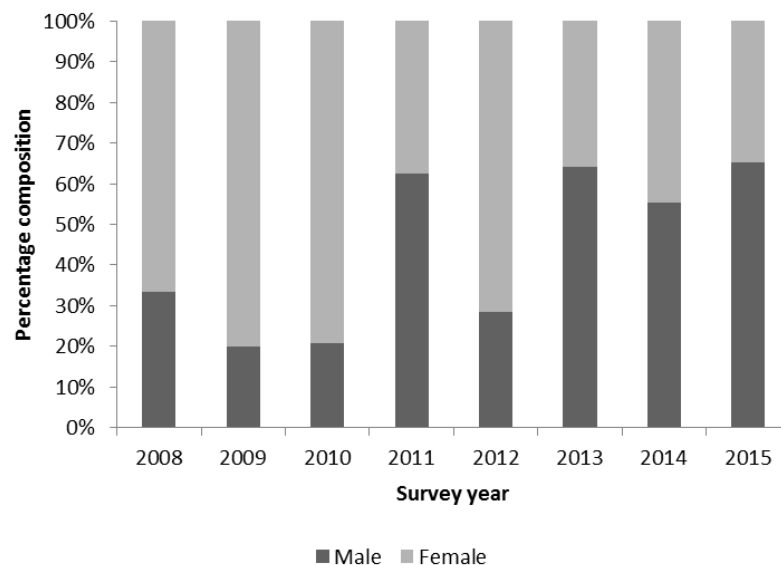


Fig. 2.11 Male to female percentage ratios varied over survey years with more females present in catches in 2008, 2009, 2010 and 2012 while males represented the majority in 2011, 2013, 2014 and 2015

No Stage 1 (immature) or Stage 7 (spent) fish were found in any of the surveys carried out. Stage 4 was the most frequently recorded maturity stage in both males (n=294) and females (n=249), representing 44.5% and 63.8% of the fish sampled respectively (Appendix 1.3). Stage 6 maturity in females was only observed in a single specimen from the 2013 survey, while it was recorded in three (18.5% of total males), four (2.4%) and six (13.3%) male specimens from the 2013, 2014, 2015 surveys, respectively. Females were found to be at a more advanced stage of maturity than males, accounting for survey year sampled (ANCOVA; $p < 0.001$). The number of maturity stages in a given cohort has increased significantly over time, from 2008 to 2015, in both sexes (ANCOVA; $p < 0.001$) (Fig. 2.12).

Values for GSI were recorded for fish from the 2015 IGFS, with female GSI ranging between 0.2% and 4.6% (mean = 1.78%; SD = 0.87%) and males ranging between 0.3% and 5.51%, (mean = 1.53%; SD = 0.92%). Females were found to have a higher mean GSI value than males across every comparative stage of maturity. No significant difference between GSI values was observed in respect of fish length or sex (ANCOVA; $p > 0.05$).

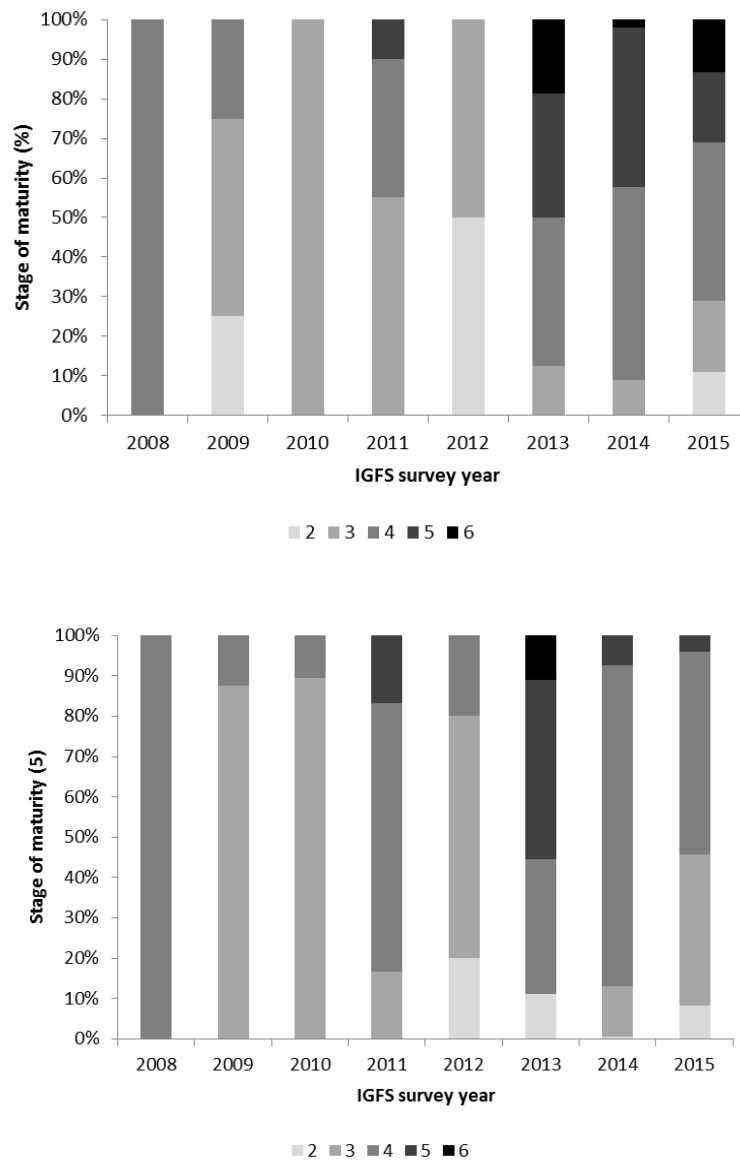


Fig. 2.12 Distribution of maturity stages in males (top) and females (bottom) of fish from 2008 to 2015 IGF surveys recorded more sexually mature fish in 2013 than other years

Stomach contents and vacuity results

Analysis of the stomach contents of sea bass from IGFS 2015 found 71.1% (n=30) of fish had some contents (whole or partially digested but identifiable fish, in addition to other non-identified contents) within their digestive tract, while none were observed in the remainder (28.9%, n=20). A species identification key onboard the *MRV Celtic Explorer* was used to identify consumed prey and found that 18 sea bass were identified as having predated on horse mackerel (*Trachurus trachurus*), while one fish having consumed a juvenile haddock

(*Melanogrammus aeglefinus*). It was found that 35.6% of male sea bass had empty stomachs compared to only 15.7% of females. There was a negative correlation between vacuity and fish length, suggesting that smaller sea bass were feeding less than larger specimens and this was observed to be more prevalent in smaller females than in males (ANCOVA; $p < 0.05$).

Discussion

The IGF surveys indicate that during November maturing sea bass of both sexes are found in aggregations in a specific area within the eastern Celtic Sea, south of St. George's Channel. Mapping of sea bass IGFS stations has revealed that the majority of the fish are captured within an area of approximately 14209km², the centre of which is approximately 90km south-south-east of the coastline of Co. Wexford. It is significant that they are not found anywhere else around the coast of Ireland, with the exception of a few fish recorded in inshore waters off the south-west coast and the sparse catches reported from the NIGFS in the Irish Sea. Similar aggregations form the basis for targeted winter fisheries in the Bay of Biscay, English Channel, southern North Sea and Western Approaches (ICES, 2013; 2015). It would appear that sea bass caught during the annual IGFS in the Celtic Sea are an extension of the fish found aggregating in the Bristol Channel (Jennings & Pawson, 1992). Integrated data from research surveys undertaken by various EU nations from 1988 to 2016 shows that the highest density of sea bass catches are recorded in the eastern English Channel with up to 700 fish per survey station (ICES, 2016b). However, it can also be observed that there are concentrated aggregations of sea bass in the Bay of Biscay and also significantly, in respect of our study, in the Bristol Channel (Fig. 2.13). As a consequence, it is not unreasonable to assume that the sea bass documented by the IGFS and those in the Bristol Channel comprise a single breeding population and that therefore sea bass in Irish waters are similar to those found within other regions in the Celtic Sea.

Migration in fish species is influenced by external drivers such as predation and spawning opportunities, in addition to internal motivators such as size, energetic status and maturity levels (Secor, 2015). The distribution of sea bass found in this study may therefore be due to a combination of three factors: migration to spawning locations, predatory behaviour and/or the optimisation of growth rate through the autumn/winter period. The waters of the Celtic Sea and Bristol Channel retain heat more efficiently than those at more northern latitudes, such as in the Irish Sea, and are subject to less fluctuation in environmental factors, such as salinity and temperature, than inshore locations (Fig. 2.3). Movement of sea bass to spawning areas can be observed in the seasonality of commercial bass fisheries operating in the Bristol Channel, particularly off the southern Welsh coastline, which have reported an increase in catches of sea bass during September to November (Pickett & Pawson, 1994). These results have also been corroborated by tag/recapture studies on the western coast of Britain which found that the fish tagged off the north-east Welsh coast travelled as far south as France in order to spawn (Kelley, 1979).

Tag/recapture results of sea bass in Irish waters have resulted in inshore recaptures in all (Kennedy & Fitzmaurice, 1972) but one case (Pawson *et al.*, 2007). Prevailing climatic conditions can influence migration distance during these early winter and spring months, with warmer periods resulting in shorter migrations due to extended inshore feeding (Pickett & Pawson, 1994). The maturity stages observed in sea bass sampled from 2008 to 2015 show a dominance of stage 3 and stage 4 in both males and females, which is in accordance with the findings of Pawson & Pickett (1994), which found that the onset of gonad maturation occurred in September/October. The distribution of maturities recorded, and the absence of any juvenile (immature) or spent fish (post-spawning), would suggest that these fish are therefore pre-spawning aggregations. Male sea bass are able to attain sexual maturity quicker and can remain at a higher state of maturity for longer when compared to females (Pawson &

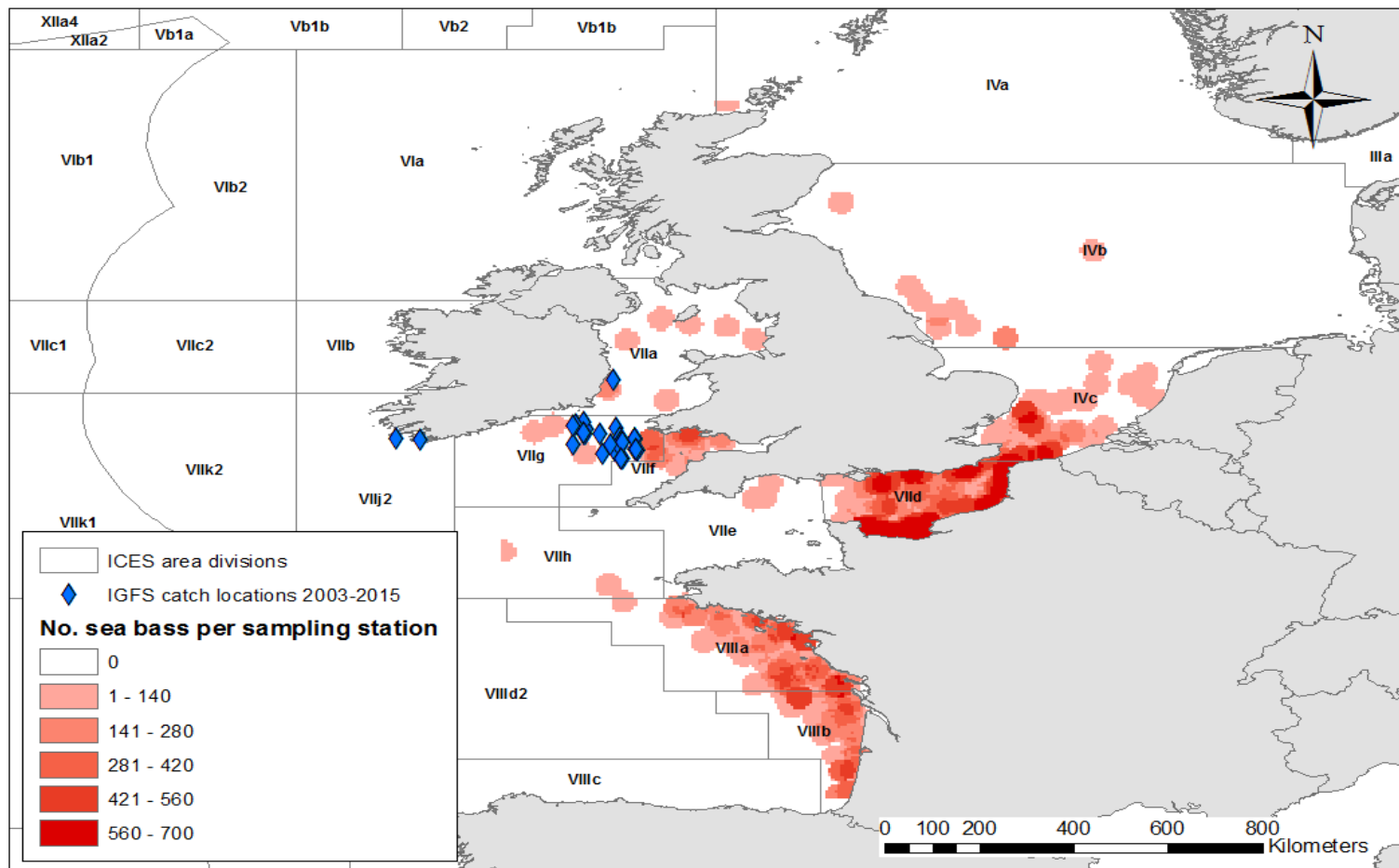


Fig. 2.13 The distribution sea bass catch locations identified in this study suggests that the sea bass encountered by the annual IGFS are part of a spawning aggregation which extends from the Bristol Channel to the south coast of Ireland. Evidence of other aggregations of sea bass are have been reported through surveying at sampling stations in the English Channel and Bay of Biscay (ICES, 2016b)

Pickett, 1996). The low counts of males and females in advanced stages of sexual maturity (stage 5 and stage 6) also suggest that spawning events may occur at a later time than when the surveys are conducted. Additionally, GSI values recorded in fish from IGFS 2015 are in accordance with the values which may be expected at the onset of development, as suggested by Pawson & Pickett (1996) further suggesting that the aggregations of sea bass are that of pre-spawning fish.

Changes in the distribution of prey species may also contribute to the observed localisation of sea bass distributions at offshore locations. Compared with juvenile sea bass, adult fish in offshore waters are generalist opportunists when foraging, becoming more piscivorous as chance encounters with large shoals of pelagic fish are increased (Spitz *et al.*, 2013). Additionally, adults often consuming fewer but larger, more nutritional prey items (Kelley, 1987). The clustered distribution of sea bass catches observed from the IGFS data may be partially related therefore to the distribution of suitable prey species for sea bass in the offshore waters of the Celtic Sea. For example, adult herring, *Clupea harengus*, are present off the south-eastern coast of Ireland, in the vicinity of IGFS sea bass stations, during winter in pre-spawning and spawning shoals (O'Sullivan *et al.*, 2013; Volkenandt *et al.*, 2014). The presence of stomach contents in most of the sea bass from IGFS 2015 showed that active feeding occurred within the area of capture. Additionally, catches from sea bass stations on IGFS 2015 were predominately juvenile horse mackerel (*Trachurus trachurus*), further suggesting that feeding was taking place. The presence of sea bass larvae to the east of the recorded IGFS catches during May suggests that the aggregations of fish were pre-spawning shoals which gathered in the area to feed, increasing energy reserves for gonad maturation later in the spawning season (Jennings & Pawson, 1992).

Sea bass which remain inshore in late autumn/winter periods are typically subjected to deteriorating feeding environments due to reduced foraging opportunities and a decrease in water temperatures (Pickett & Pawson, 1994). As a result, growth during this period is

limited, with high numbers of fish with empty stomachs having been recorded in inshore specimens during winter (Pickett & Pawson, 1994). While migration results in the expenditure of significant energy resources, this expenditure may be offset by increased foraging opportunities on more abundant prey species in more southerly waters. The warmer water temperatures found at more southerly offshore locations, such as those displayed in Fig. 2.3, also may result in an increased metabolism, allowing for increased feeding levels compared to colder inshore waters or northerly waters (Pickett & Pawson, 1994). The consistent drop in growth increments observed in fish aged six years or more (Pawson & Pickett, 1987) is also evident in this study, with development of gonads and the undertaking of annual migrations diverting energy from older fish growth when compared to juvenile and adolescent sea bass (Pickett & Pawson, 1994).

The sea bass recorded on IGF surveys were all deemed to be adults based on recorded lengths. Both male and female bass are deemed adults in north-west Europe when attaining a total length of over 42cm (IFI, 2014). Females were found to have a significantly higher length/weight relationship than males across survey years, in accordance with previously published literature (Pawson and Pickett, 1996). Similar estimated length at ages were also observed between the sexes up to five years of age, however females older than five years grew significantly quicker than males of the same age; this was also reported by Pawson & Pickett (1996). This increased growth rate beyond five years of age is believed to be attributed to the necessity for accommodation of proportionally larger gonads for females with increasing age than compared with males, which offers females a reproductive advantage as fecundity is positively related to body size (Wassef & Emary, 1989). Interestingly, the occurrence of significantly higher condition indices in fish from IGFS 2014 and 2015 coincides with elevated sea surface temperature (SST) at catch locations, suggesting that condition may be related to water temperature. This relationship may be due to elevated growth rates and feeding opportunities associated with the warmer offshore

waters though analysis of final year estimated mean length increases for both males and females from both years found no significant differences.

The origin of sea bass caught at these offshore locations is currently unknown. Kelley (1979) found that sea bass on the western coast of Britain migrate south at the end of autumn and into early spring to the waters of the Bristol Channel and Cornish peninsula and even as far south as the French coastline. Evidence of mixing between sea bass originating in Irish and British waters has also recently been recorded through the use of tagging programs (Pawson *et al.*, 2007). The presence of a tagged sea bass of Irish origin within the locality of IGFS catches documented in this study has also been confirmed (Pawson *et al.*, 2007), suggesting that sea bass from both Britain and Ireland may be the source of spawning aggregations in this region, which was also suggested by Fahy *et al.* (2000).

However, the extent to which interconnectivity exists between sea bass originating from both British and Irish nursery areas in spawning aggregations is unknown. The absence of a commercial fishery for sea bass within Irish inshore waters, in conjunction with low directed fishing effort by other EU nations within Irish offshore waters (ICES, 2013b), contributes to poor returns from tag/recapture studies and therefore poor knowledge of the potential migratory paths of the species within Irish offshore waters. A study of sea bass in Irish inshore waters found females outnumbered males by a ratio of 2:1 (Kennedy & Fitzmaurice, 1972) while overall ratio of males to females from this study was biased towards males (51.4%), with the sex ratio differing throughout survey years (Fig. 2.9). While this may suggest that sea bass populations in Irish waters may differ in composition to those found offshore in the Celtic Sea, the prevalence of males in offshore samples is most likely due to early maturity of gonads and therefore early migration to offshore aggregative areas. The dominance of females in the 2012 catch coincides with the lowest mean SST for the past four years (12.6°C) while the warmer years of 2013 to 2015 were found to have a male majority. This suggests that water temperature may influence spawning aggregation sex ratios, with

males more prevalent in warmer waters (in accordance with the findings of Vandeputte *et al.*, 2012), however care must be taken when interpreting this result due to the low numbers of fish caught in 2012 ($n = 7$).

It is possible that the differences in age composition and structure of fish caught on different surveys were as a result of the aggregation of sea bass being comprised of fish from different locations. Mixing of sea bass from separate locations is believed to occur during migration, with specimens from lower latitudes joining shoals of sea bass migrating south from areas further north (Pawson *et al.*, 1987). Evidence of this common migration route is also noted in Pawson *et al.* (2008).

Conclusion

The sea bass catches documented by the IGFS have provided valuable data concerning the biological traits of sea bass found in Irish offshore waters. The relatively discrete distribution of the catches provides evidence of offshore aggregation of sea bass during early winter, while the biological data provided by analysed specimens are similar to the fish sampled by Pawson & Pickett (1996). It is therefore reasonable to assume that the sea bass caught on the IGFS may be an extension of the same pre-spawning aggregation identified within the Bristol Channel and that this pre-spawning aggregation within the Celtic Sea may extend from the Bristol Channel to the south coast of Ireland. Interestingly, tagging studies in British waters have revealed that aggregations of sea bass in the Bristol Channel are likely to be comprised of fish moving seasonally along the western British coast between the Solway Firth and southern Cornwall further highlighting the large geographical area over where these fish may migrate from (Pawson *et al.*, 2007). The probable reasons for the observed distribution may be due to a combination of the spawning and growth benefits associated with the ambient water temperature in the Celtic Sea in addition to changes in the distribution and abundances

of prey species. To further understand the phylogeny of sea bass found in Irish coastal waters, it is suggested that the relationship between this offshore IGFS group of fish and its likely membership of a Bristol Channel population be investigated. In this regard, both physical tagging and tracking and genetic studies would provide additional insights into the composition and origin of fish in these aggregations (see Chapter 5 and Chapter 6).

Acknowledgements

This research was supported by the Beaufort Marine Research Award in Fish Population Genetics funded by the Irish Government under the Sea Change Programme and by funding received directly from the Marine Institute. The author would like to acknowledge the help offered by members of the Marine Institute, University College Cork and the Agri-Food and Biosciences Institute of Northern Ireland (AFBINI) during this study.

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Chapter 3

Theoretical simulation of European sea bass, *Dicentrarchus labrax*, larval dispersal off the southern and eastern coasts of Ireland and the potential implications for recruitment

Abstract

Knowledge of the spawning locations of the European sea bass, *Dicentrarchus labrax*, in Irish waters is poor, although juveniles are known to recruit to estuarine habitats in autumn. In this study, the dispersal of sea bass larvae in inshore and offshore waters off the southern and south-eastern coast of Ireland was simulated using a Lagrangian particle tracking model, based on environmental data collected in 2012. The model was used to simulate dispersal of larvae from five inshore and nine offshore locations during the assumed spawning season from February to June, with simulations run using passive and diel vertical migration behaviours. In addition, differences in dispersal patterns based on particle release depth were also investigated. Based on particle tracking, it can be seen that sea bass larvae may be delivered along the Irish coastline, particularly along the south coast, from both inshore and offshore spawning locations. However, the strength of this effect varies depending on geographical location and the time of release event. In general, the geographical extent of particle dispersal suggests that larval dispersal would be lowest at the start of the assumed spawning season in February and highest towards the end of this period in May and June. Dispersal distance would be greatest for larvae released at surface locations and would decrease with depth. This study also suggests that spawning locations on the south-eastern Irish coast and in offshore locations in the Celtic Sea may act as sources of larvae for localities such as south Co. Kerry which is up to 200km away, but may also be contributing towards recruitment of sea bass in Northern Ireland and south-western Scotland, thus potentially impacting on sea bass recruitment regionally, nationally and internationally.

Introduction

European sea bass (*Dicentrarchus labrax*) are an important species for commercial and recreational fisheries throughout Europe. Commercial fishing for sea bass in Irish waters

ceased in 1990 and angling is strictly regulated due to perceived low stock levels (IFI, 2014). However, little is known about the biology of sea bass in Irish waters, particularly the location of spawning sites, and as a result, the means by which eggs and larvae are dispersed and are recruited into suitable juvenile rearing habitats is currently unknown.

Previous studies have found that sea bass become sexually mature between the ages of four to six years (Pawson & Pickett, 1987) with females capable of producing in excess of 200000 eggs per kilogram of body weight. Research by Kennedy & Fitzmaurice (1968; 1972) has identified sea bass eggs at five locations on the southern coast of Ireland: Blasket Sound, Dingle Bay, Youghal, Waterford estuary and Splaugh Rock in inshore waters of Co. Wexford which were suggestive of spawning activity at these locations. Long-term observations of sea bass by the Irish GroundFish Survey (IGFS) in offshore waters have identified a substantially discrete, aggregation of pre-spawning sea bass in the eastern Celtic Sea (see Chapter 2), which could be an important source of juvenile sea bass recruitment into Irish coastal waters, assuming adult fish spawn at this offshore locality. The presence of sea bass larvae within this offshore region has been previously identified (Jennings & Pawson, 1992; Dransfeld *et al.*, 2000).

It is believed that sea bass larvae need to move inshore to seek appropriate nursery areas in which to continue their development. The use of inshore coastal waters by juvenile sea bass is likely linked to their higher productivity, which is associated with the abundance of prey species, among other factors such as refuge from predators and optimal environmental conditions for growth (Aprahamian & Barr, 1985), with habitats such as estuaries and lagoons favoured. The process by which sea bass larvae migrate into inshore nursery zones is poorly understood (Pickett & Pawson, 1994). While the embryos are believed to initially float post-fertilisation, the larvae soon sink and can occupy different depths within the water column (Pickett & Pawson, 1994). A survey carried out by Pickett & Pawson (1994) in the Bristol Channel deployed surface buoys to locations where larvae were present to investigate

the potential transport routes of larvae to inshore nursery zones. While the drifters did move towards suitable nursery habitats, they did so at a slower rate than would be expected based on the stage of development of larvae sampled within these inshore zones. This evidence has suggested that sea bass larvae may use sub-surface currents and selective tidal stream transport to accelerate their transport to nursery zones.

There is some evidence that fish larvae can perceive pressure and depth, and therefore potentially regulate their place within the water column preferentially (Grioche *et al.*, 2000; Huebert, 2008; Huebert *et al.*, 2010). There is also some research to suggest that larvae adopt diel vertical migration (DVM) as a means of influencing their transportation to nursery locations (Grioche *et al.*, 2000). Secor (2015) has suggested that similar species, such as Japanese sea bass, *Lateolabrax japonicas*, may use tidal stream transport into estuarine regions, but that there was not sufficient evidence to confirm this. Additionally, the use of DVM behaviour has been observed in the larvae of numerous species (Grave, 1981; Clark & Levy, 1988; Haldorson *et al.*, 1993; Auditore *et al.*, 1994). This behaviour, the daily movement of larvae through the water column with respect to luminosity levels, has been found to limit the dispersal of larvae due to the daily vertical migrations (Grioche *et al.*, 2000). Passive behaviour as a means of larval transport suggests usage of oceanic currents, tides and other physical processes to disperse larvae away from spawning locations. Such behaviour may allow for the easier selection of sub-surface oceanic currents to facilitate faster transport to inshore nursery zones.

Direct observations of individual larval migration are time and resource consuming (Edwards *et al.*, 2008). Traditionally, surveying of fish eggs and larvae was restricted to towing plankton nets and analysing the resultant catch. The results from this method, while indicative of the presence of larvae in a given area and at a particular time, fail to take into account the change of the composition of larvae over temporal and spatial scales (Edwards *et al.*, 2008). In particular, the behaviour of fish larvae may affect their presence within the

water column at a given time, diurnally or seasonally, and therefore may be a poor representation of their actual abundance. Recent years have seen the development of modelling as an approach to simulate the dispersal of eggs and larvae from user-defined release sites. These models use ‘particles’ or ‘virtual larvae’ constrained within a pre-defined boundary, in which spatial and temporal environmental data are available to simulate the movements of actual larvae. These simulations can provide valuable insights into how the larvae might disperse from a given point and at a given time (Edwards, 2006). The addition of a particle behavioural component into these models increases the realism of the simulation, allowing the user to define the type of movement the particle will adopt.

The primary objective of this study was to (i) simulate potential dispersal of sea bass larvae for a number of inshore and offshore spawning scenarios using a simulated particle model. Given that there is uncertainty regarding the spawning time of sea bass in Irish waters, (ii) spawning scenarios at different times of the year were also simulated. Furthermore, to account for the possibility that larval sea bass can actively select which depth they can occupy, (iii) the potential for variation in dispersal patterns of larvae released at a number of different depths within the water column was investigated. Finally, the results of simulated larval dispersal (iv) at historically identified potential nursery locations were compared, based on reported sea bass egg presence in Kennedy & Fitzmaurice (1972), in the south-east of Ireland.

Material and methods

Particle release sites

Offshore particle release locations were chosen on the basis of data collected between 2003 and 2016 from the Irish GroundFish Survey (IGFS), which is carried out by the Marine

Institute annually and also from discard monitoring (monitoring of at-sea disposal on board commercial fishing vessels of non-retained species due to low commercial value or absence of sufficient quota) (see Chapter 2). Particle start locations for inshore modelling simulations were chosen on the basis of known sea bass angling hotspots along the south and east coast. The locations (GPS coordinates) of Commission for Irish Lights (CIL) inshore navigation buoys, which were situated close to areas with a reputation for productive sea bass angling, were used as a valuable reference point to fix potential inshore spawning sites. Dispersal of larvae was also simulated based on location data provided by a sea bass tagged with a pop-off satellite archival tag (PSAT) (Fig. 3.1). The PSAT location was taken from data provided during the peak spawning period during May and June (see Chapter 5) and these data were analysed separately to the other inshore and offshore outputs.

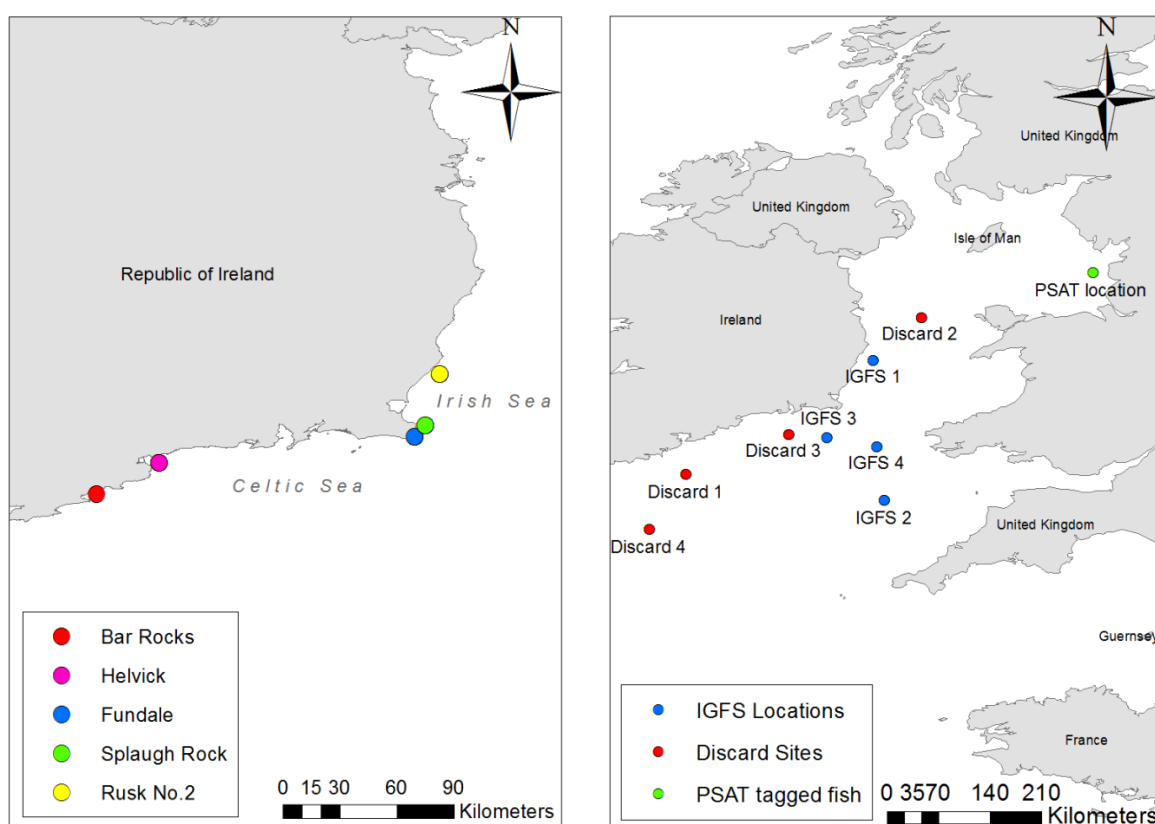


Fig. 3.1 Locations of initial particle start locations for inshore and offshore sites

Once released into the water column, sea bass eggs may be transported towards inshore areas. Upon hatching of successfully fertilised eggs, the juvenile larval stage of sea bass may last for a period of approximately 30 to 90 days (average = 60 days) (Kelley, 1988). The spawning season in the Celtic Sea is believed to occur between February and June (Pickett & Pawson, 1994). Therefore, individual simulations of 60 days duration were modelled for each release site commencing in the months of February, March, April, May and June. Simulations were run using 1000 particles, allowing for five separate bins of 200 particles. To investigate the potential differences in dispersal based on release depth, each 200 particle bin was assigned to a different depth depending on inshore or offshore spawning simulations. For inshore locations, the depths were: 0m (surface), -5m, -10m, -15m and -20m. Particles at offshore locations were split into depths of: 0m (surface), -5m, -10m, -20m and -50m. The deeper depth for offshore sites is appropriate given that Sabatés (2004) found sea bass larvae at depths of 50m.

The model

The three-dimensional Regional Ocean Modelling System (ROMS) was used to simulate the environmental conditions within the study area of the Celtic Sea and Irish Sea. ROMS is a free-surface, three-dimensional, terrain-following oceanic model which adopts the use of specific hydrostatic and Boussinesq assumptions (Haidvogel *et al.*, 2008; O’Sullivan *et al.*, 2015) and was developed by the Rutgers University in UCLA (California, USA). The Marine Institute developed a ROMS model for Irish territorial waters, in addition to those of the north-east Atlantic, which includes data for water temperature and salinity transport models. Further description of the Marine Institute ROMS can be found in O’Sullivan *et al.* (2013; 2015).

The Larval TRANSport Lagrangian model (LTRANS), written in Fortran 90, is an offline particle tracking model developed to run on data generated by ROMS and which is suited to high-performance computing. This modelling software was designed by Elizabeth North and Zachary Schlag of the University of Maryland Center for Environmental Science, Horn Point Laboratory, USA. The version used in this study is LTRANSv.2b (North *et al.*, 2011). The model incorporates a number of features to plot the trajectory of particles subject to physical factors and behavioural responses such as active settlement selection and movement in tidal streams only. At each time step, the movement of particles is predicted based on recorded advection (physical oceanographic processes) and turbulence data in addition to predefined larval behaviour. The advection and turbulence data is stored as NetCDF files and is based on environmental data for the Celtic and Irish Sea for the year 2012. A full description of model functionality and LTRANS is available in Schlag & North (2012).

LTRANS has an additional random component added to particle motion in order to replicate turbulence at resolutions smaller than grid level (Hunter *et al.*, 1993). A random displacement model is used to calculate particle motion in the vertical direction as a result of turbulence, while a random walk model is used to add particle motion horizontally.

Environmental data

The post-hatching rate of development of sea bass larvae is believed to be closely related to water temperature with a sea surface temperature (SST) of 8.5°C to 9.0°C being recognised as the minimal threshold and 15°C as the upper threshold at which larvae and eggs are found in the wild (Thompson & Harrop, 1987). Outside of this temperature range, successful spawning is not believed to occur in the Celtic Sea (Pickett & Pawson, 1994). SST values were extracted from modelled environmental data from the year 2012 (Appendix 2.1 to 2.5)

and are the basis upon which hatching times and development rates of particles during different simulations were calculated (Table 3.1).

Table 3.1 Temperatures (°C) at release sites for first day of each month (temperatures below 8.5°C = blue; above 15°C = red)

Release sites	February	March	April	May	June
Bar Rocks	7.5	10.2	10.5	10	16.4
Fundale	8.2	8.8	10	9.9	13
Helvick	6.3	9.6	10.5	9.9	14.6
Rusk No.2	7.4	8.2	10	9.8	15.1
Splough Rock	8.1	8.8	10	9.9	13.1
Discard 1	9.9	10.8	10.8	10.2	14.7
Discard 2	9.2	8.6	8.9	9	13.4
Discard 3	9.8	9.6	10.5	9.8	14.7
Discard 4	10.8	10.8	11.3	10.7	14.3
IGFS 1	7.7	7.5	8.9	9.8	12.3
IGFS 2	10.5	10	10.1	10.6	15.3
IGFS 3	10	9.8	10.3	9.7	12.8
IGFS 4	10.2	9.3	9.5	9.8	14

The SST at each particle release site suggested when swimming behaviour might begin, with higher SST values allowing for accelerated development of the eggs and the timing of hatching and, therefore, a reduced time prior to the commencement of swimming behaviour. Hatching time at higher water temperatures (15°C) was assumed to be approximately four days, increasing to approximately nine days in waters at 9°C. At hatching, while measuring approximately 4.0-4.5mm long (Pickett & Pawson, 1994), sea bass larvae possess the ability to swim (Olivier *et al.*, 2013). The swimming speed of wild sea bass larvae is unknown, though plaice (*Pleuronectes platessa*) larvae in cold temperate waters have been observed at speeds of up to 30 body lengths per second (BL/s⁻¹) for short periods (Osse & van den Boogaart, 1995). For species in cool temperate waters where swimming speeds are not known, Staaterman & Paris (2013) suggest that a speed of five to 10BL/s⁻¹ can be used. On this basis, a conservative swimming speed of 0.02125m/s⁻¹ based on a mean length of

4.25mm was calculated (using the lower 5BL/s^{-1}). The maximum swimming speed of the larvae is 0.0625m/s^{-1} based on an estimated length, 60 days post-hatching, of 12.5mm. Sensitivity analysis of the model was carried out using initial larval swimming speeds of 3BL/s^{-1} , 6.75BL/s^{-1} and 10BL/s^{-1} also. The model calculated a linear change in swimming speed over the 60 day simulation period, depending upon particle age, by specifying a slope and intercept defined by the parameters swimfast (the maximum swimming speed), swimslow (initial swimming speed), and swimstart (time after simulation start in seconds), which are specified in the input file (Schlag & North, 2012).

Particle behavioural component

To investigate the effects of a) physical oceanographic processes as a means of larval transport and b) the daily movement of larvae through the water column, with respect to luminosity levels, on potential larval dispersal, modelling simulations were run using both DVM and passive behaviour separately to allow for comparison of outputs.

For both DVM and passive behaviours, particle mortality was turned off to allow for visualisation of maximum particle dispersal. Luminosity levels for DVM behavioural simulations were calculated based on twilight data from the UK Hydrographic Office (HMNAO, 2015) and from solar irradiance levels obtained from the Irish national weather agency, Met Éireann.

Data analysis

Outputs from LTRANS for each spatial, temporal and behavioural combination were plotted using ArcMap 10.0. The median centre of the particle dispersal cloud was used to calculate distance travelled and average velocity for particles for each simulation. Dispersal area of the

particle cloud was calculated using an ellipsoid of one standard deviation, which encompassed the core 68% of the total area covered, indicating the estimated central location and size of potential larval dispersal. In scenarios where the ellipsoid overlapped with a landmass, the area of overlap was subtracted from the ellipsoid area total. Particle density within the ellipsoid was calculated using the following equation:

$$\frac{\text{Number of particles within ellipsoid } (n)}{\text{Area of ellipsoid in km}^2 (a)}$$

where n is the number of particles represented by the ellipsoid and a is the area of the ellipsoid in square kilometres (km²). In overall monthly scenarios with 1000 starting particles, $n = 680$ given the area covered by the ellipsoid to one standard deviation (i.e. the core 68% of estimated dispersal of the 1000 particles). However, when analysing split depth particle release results with 200 starting particles at each depth, the ellipsoid covered the core 68% of the 200 particles released at that depth ($n = 136$). Model output was compared under the following parameters:

1. Mean distance of particle travel: Measured in kilometres from the release location to the median centre of the ellipsoid
2. Mean particle velocity: Measured in kilometres/day⁻¹
3. Mean area of particle dispersal: Calculated as the area of the ellipsoid. In cases where the ellipsoid overlapped with a landmass, the overlap value was deducted
4. Mean particle density: The number of particles per square kilometre (km²)

Relationships between the recorded results of these parameters for each different simulation run and each location and time were compared using a two-way ANOVA. Dispersal extent of particles was analysed to investigate the potential retention of larvae within historic areas on

the south-east coastline (Fig. 3.2), identified in Kennedy & Fitzmaurice (1968; 1972). The possibility of the retention of particles within these areas was confirmed if during the course of the 60 day simulations, a particle came within 3km of the designated locations, which was calculated using ArcGIS (Version 10.2)

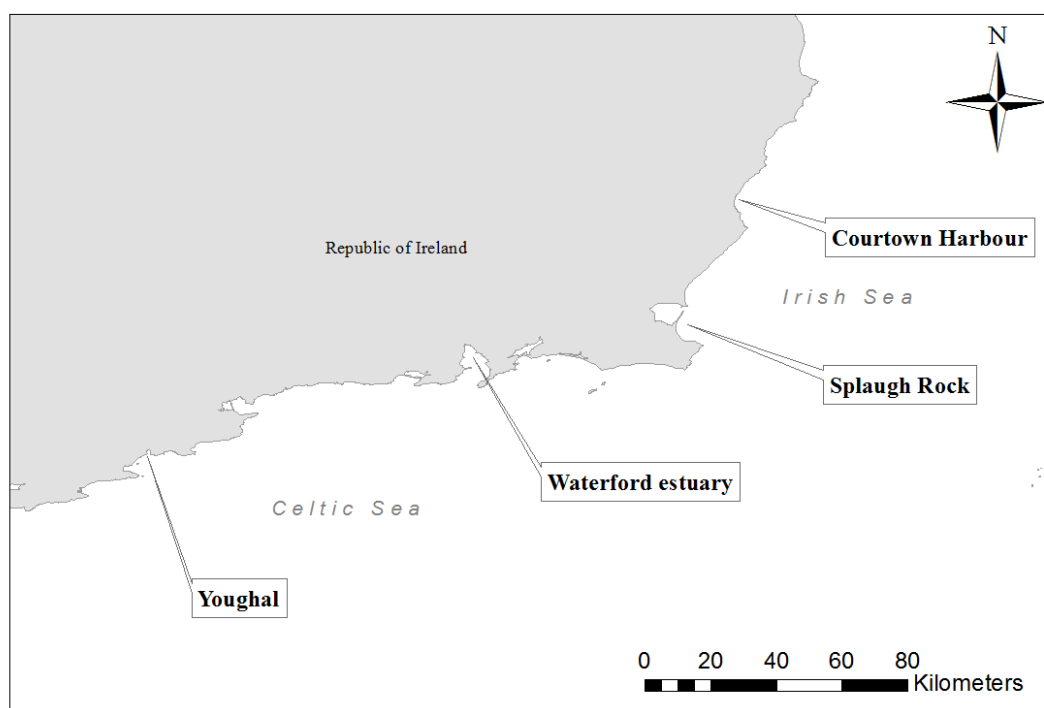


Fig. 3.2 Historic egg and larval locations within the southeast of Ireland

Results

Inshore and offshore release sites

Sensitivity analysis of model output based on different swimming speeds for no significant difference in dispersal area or particle distance covered (ANOVA, $p > 0.05$). There was no significant difference in mean distance, mean velocity, mean area of dispersal and mean density in DVM behaviour simulations for inshore sites both between spawning locations and between months (Table 3.2). While passive behavioural simulation analysis showed no significant difference in mean density between locations and across months, a significant

difference ($p < 0.05$) was observed between locations in mean distance and mean velocity while a highly significant difference ($p < 0.001$) in mean area was found. For offshore locations, highly significant ($p < 0.001$) differences in mean distance, velocities, areas and densities were recorded among spawning months based on DVM behaviour, with further notable differences concerning mean distances and velocities present between locations. Analysis of passive dispersal of particles found no significant difference among sites in respect of mean particle densities, however, all other aspects showed significant variances.

Table 3.2 Two-way ANOVA results (p-values) comparing resulting mean distance, velocities, area and particle density between the locations of inshore release sites ($n = 5$) and offshore release sites ($n = 8$) and spawning months ($n = 5$)

	DVM		Passive	
	Between month	Between location	Between month	Between location
Inshore mean distance	>0.05	>0.05	0.05	0.05
Inshore mean velocity	>0.05	>0.05	>0.05	0.05
Inshore mean area	>0.05	>0.05	0.05	0.001
Inshore mean density	>0.05	>0.05	>0.05	>0.05
Offshore mean distance	0.001	0.05	0.001	0.05
Offshore mean velocity	0.001	0.05	0.001	0.05
Offshore mean area	0.001	>0.05	0.001	0.001
Offshore mean density	0.001	>0.05	>0.05	>0.05

Particles originating from the Fundale release site during April exhibited the highest mean velocity recorded for both behaviour types (DVM = 3.42km/day^{-1} ; Passive = 4.35km/day^{-1}) and the furthest mean distance travelled (DVM = 205.3km ; Passive = 260.8km). Additionally, both DVM and passive outputs showed that February had the lowest mean distance covered and average particle velocity (DVM = 42.86km at 0.71km/day^{-1} ; Passive = 61km at 1.01km/day^{-1}) in addition to having the lowest mean area of dispersal (DVM = 1436.35km^2 ; Passive = 3937.87km^2) (Fig.3.3, top and bottom left respectively). DVM based simulations for the month of May were found to have the largest mean area of dispersal (3428.16km^2) (Fig. 3.3, top right), while for passive behaviour June (15737.68km^2), resulted in the largest mean areas of dispersal (Fig. 3.3, bottom right). For both behaviours, Rusk

No.2 was the location which had the lowest mean dispersal area (DVM = 1455.67km^2 ; Passive = 992.08km^2), in addition to the highest mean density of particles (DVM = 0.49 per km^2 ; Passive = 23.1 per km^2) at the end of the 60 day simulations.

The spawning locations with the lowest mean velocities for particles and with the shortest mean distance of particle travel recorded were to be found at Splaugh Rock (DVM = 37.28km at 0.62km/day^{-1}) and at Rusk No.2 (Passive = 45.66km at 1.78km/day^{-1}) on the eastern coast. Splaugh Rock also had the highest mean area of dispersal and lowest mean density of particles in DVM (3468.67km^2 at a density of 0.28 particles per km^2) based simulations, while in passive behaviour simulations, the lowest mean dispersal area and density of particles occurred at Bar Rocks (16251.94km^2 at a density of 0.05 particles per km^2). February showed the highest mean density of particle concentration in DVM behaviour simulations (0.55 particles per km^2), but passive simulations indicated that in June the densest particle clouds were present, having a mean of 21.31 particles per km^2 , a magnitude of 18 times the cloud density of the next closest month (March at 1.17 particles per km^2).

The highest mean distance travelled and mean particle velocity for offshore particle simulations were observed in June (DVM = 132.24km at 2.2km/day^{-1} ; Passive = 120.35 at 2.01km/day^{-1}) (Fig. 3.4, top and bottom right respectively). Additionally, June was found to have the largest mean area of dispersal and the lowest mean density for both behavioural types (DVM = 10650.6km^2 at a density of 0.1 particles per km^2 ; Passive = 18090.48km^2 at a density of 0.07 particles per km^2) (Fig. 3.4). The lowest mean particle velocity and mean distance of particle travelled for offshore release sites was found in February for both DVM (39.23km at 0.65km/day^{-1}) and passive (34.36km at 0.57km/day^{-1}) behaviours (Fig. 3.4, top and bottom left respectively), while March had the highest mean density of particles observed across all possible spawning months (DVM = 0.4 particles per km^2 ; Passive = 0.65 particles per km^2). Particles originating from the release site Discard 3, located off the southern coast of Co. Waterford, were found to have the highest mean particle velocity/distance travelled

(DVM = 145.76km at 2.43km/day⁻¹; Passive = 139.04km at 2.32km/day⁻¹). In contrast, particles originating from Discard Site 4 travelled the shortest mean distance (DVM = 48.42km; Passive = 57.04km). The highest mean density of particles was recorded at IGFS 1 in the Irish Sea for both DVM (0.4 particles per km²) and passive (1.26 particles per km²) behaviours. The high density of particles at IGFS 1 for passive simulations coincides with the lowest mean dispersal area attributed to particles released from that site across all months (2177.92km²), though DVM simulation outputs showed Discard Site 3 had the lowest particle mean dispersal area (2782.72km²).

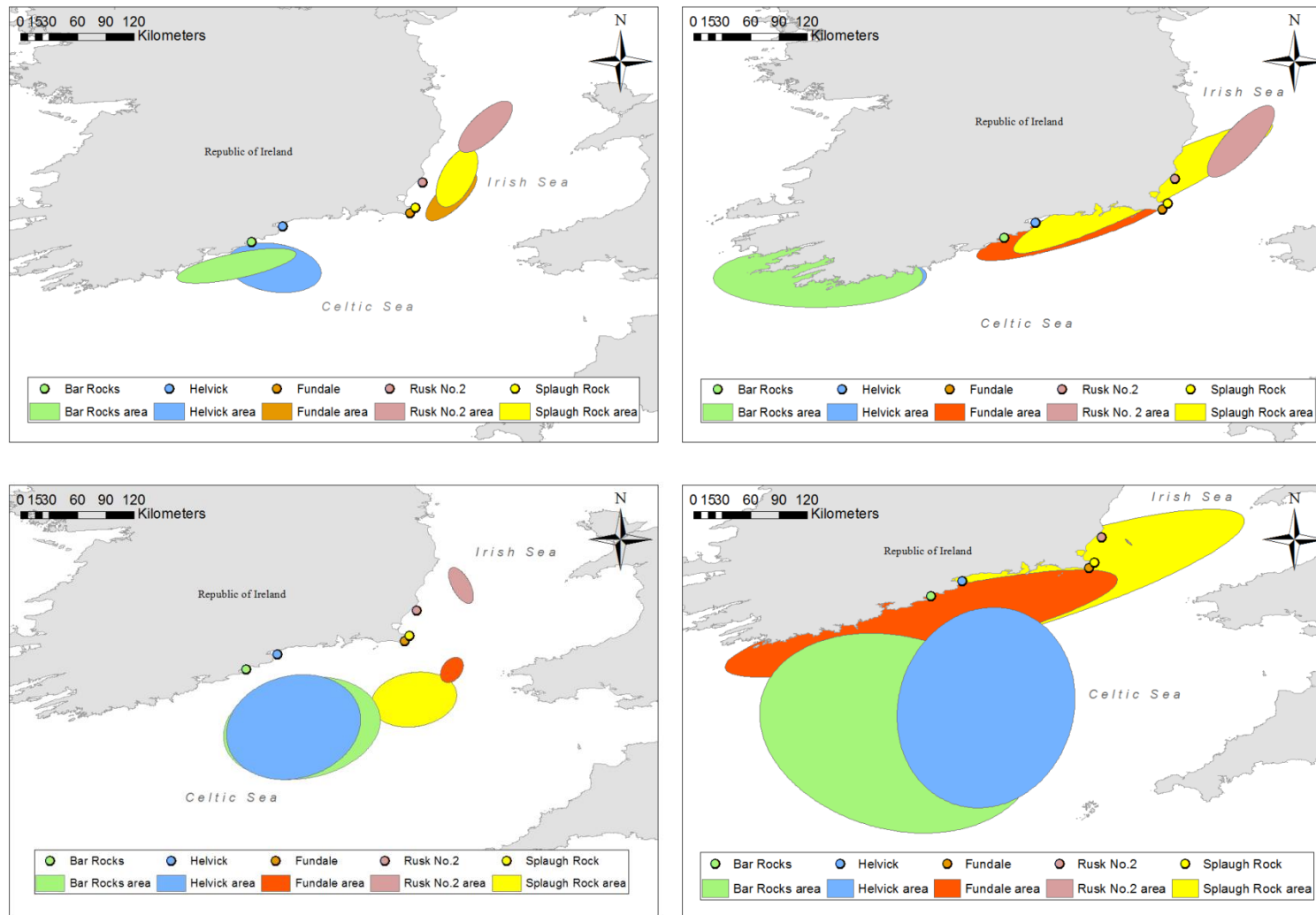


Fig. 3.3 Predicted dispersal areas of particles for DVM behaviour in February (top left) and May (top right) and for passive behaviour in February (bottom left) and in June (bottom right) for inshore release sites found a general trend of increased dispersal area in the later months of simulation

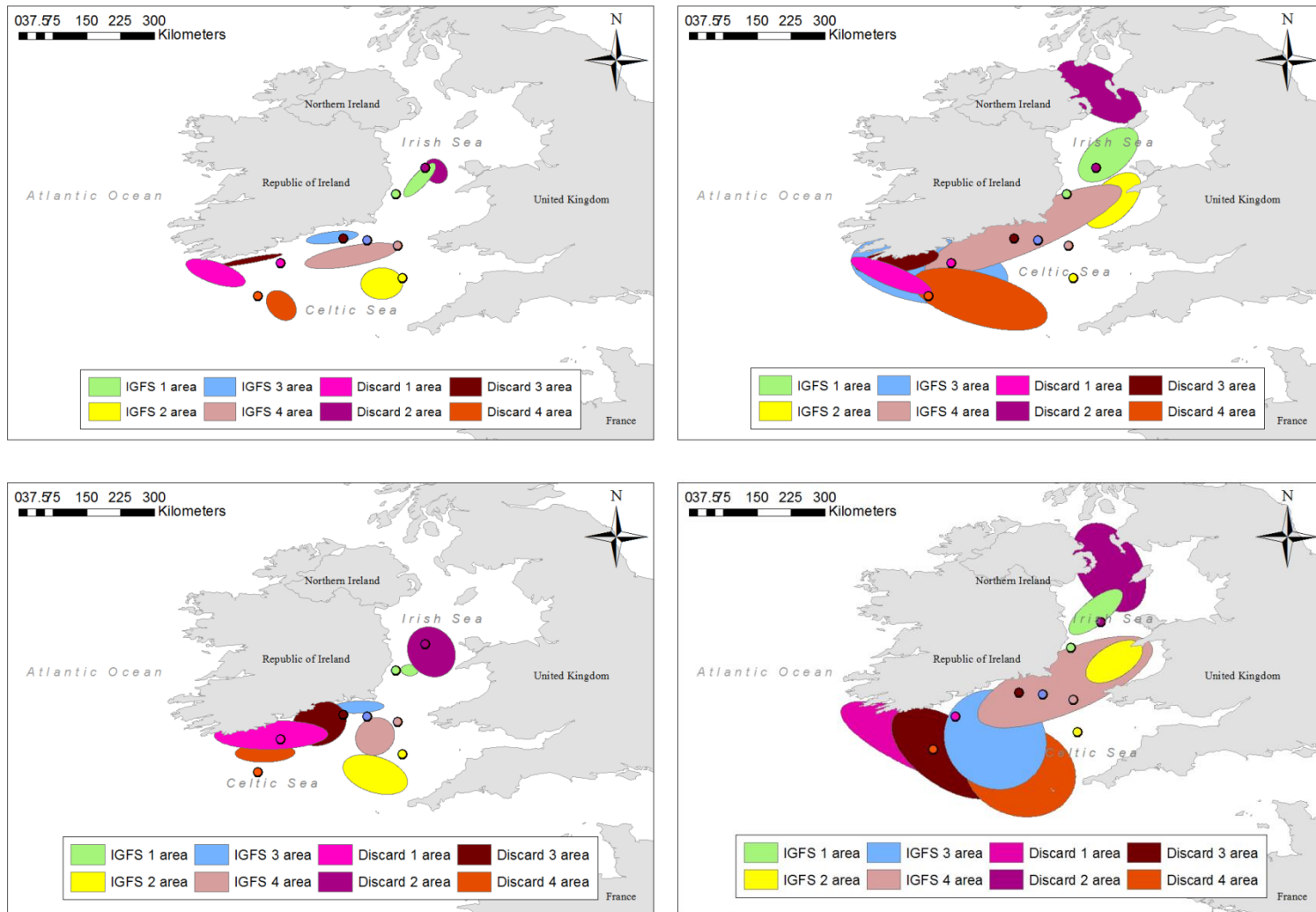


Fig. 3.4 Predicted dispersal areas of particles for DVM behaviour for March (top left) and June (top right) and for passive behaviour for February (bottom left) and June (bottom right) for offshore release sites (Corresponding release site denoted by coloured circle)

Split depth results

No significant difference in the density of particles was found for either DVM or passive behaviours at different depths (Table 3.3). The mean distance of particle travel and mean velocity did not differ for DVM behaviour at separate depths. In contrast, statistically significant differences were found for passive behaviour at the various simulated depths. Mean area of dispersal varied significantly at different depths for DVM particle release. In comparison, no significant differences were observed for passive behaviour. At offshore locations, results from split depth analysis showed a clear difference between DVM and passive behaviours. While significant differences ($p < 0.05$) in both mean distances of particle travel and mean velocities occur in simulations run using DVM behaviour, no differences were seen for passive behaviour. Similarly, while there were significant differences ($p < 0.05$) between mean particle area of dispersal and densities at different depths of release when simulations were set to passive behaviour, no such differences were observed under DVM behaviour.

Table 3.3 Two-way ANOVA results comparing resulting mean distance, velocities, area and particle density between inshore ($n = 5$) and offshore ($n = 8$) spawning locations and spawning months ($n = 5$) based on split depth ($n = 5$) release

	DVM	Passive
	Between depths	Between depths
Inshore mean distance	>0.05	0.05
Inshore mean velocity	>0.05	0.05
Inshore mean area	0.05	>0.05
Inshore mean density	>0.05	>0.05
Offshore mean distance	0.05	>0.05
Offshore mean velocity	0.05	>0.05
Offshore mean area	>0.05	0.05
Offshore mean density	>0.05	0.05

Particles released at the surface (0m) were found to have the highest average velocity (1.33km/day^{-1}) for DVM behaviour (Fig. 3.5). In addition, output from DVM simulation of surface release particles showed the largest mean area of dispersal (2265.94km^2) and lowest

average density (0.09 particles per km²). In contrast, the 200 particles released at the maximum depth at inshore sites (-20m) had the lowest average velocity (1.19km/day⁻¹), smallest average area of dispersal (1654.62km²) and highest mean particle density (0.12 particles per km²).

Inshore DVM split depth dispersal outputs, with the exception of particle density, declined from the surface layer (0m) to the bottom depth of particle release (-20m). Particles released at -20m were found to have the lowest average velocity (1.89km/day⁻¹) and smallest average area (7302.61km²) of dispersal based on passive behavioural simulations. In contrast to DVM model outputs, the lowest mean particle density was recorded at -20m (0.6 particles per km²); the highest average density being found at -10m (1.58 particles per km²). Similar to DVM, passive simulations indicated that particles released at surface level had the highest average velocity (2.18km/day⁻¹) and particles released at -5m depth resulted in the largest average area of dispersal (8144.86km²).

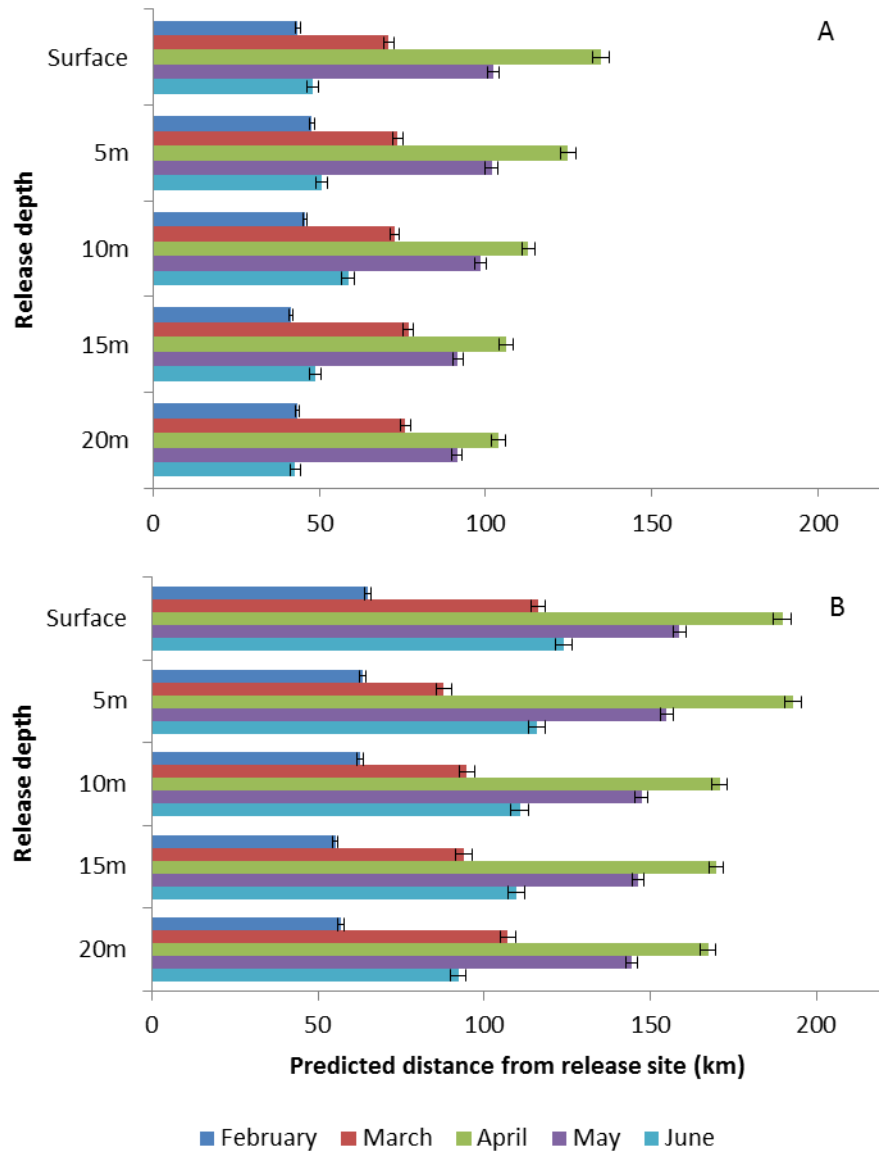


Fig. 3.5 Mean distance of particle travel (km) from release site based on depth for DVM (A) and passive (B) behaviours for inshore locations (\pm SE) for different months found that particles released at depths of -20m had the lowest mean velocity

In offshore spawning sites, the highest densities and lowest average velocities were recorded at the maximum release depth of -50m for both DVM (density = 0.09 particles per km²; velocity = 1.9km/day⁻¹) and passive (density = 0.64 particles per km²; velocity = 1.22km/day⁻¹) behaviours (Fig. 3.6). The lowest density was recorded for surface released particles (DVM = 0.07 particles per km²; Passive = 0.15 particles per km²). The highest average velocity was observed in DVM particles released at -20m (1.63km/day⁻¹), while in passive simulations this was found to be at the surface (1.69km/day⁻¹). Finally, at -5m and -20m the largest

(3242.13km²) and smallest (2716.2km²) mean areas of dispersal were exhibited under DVM behaviour respectively, while the largest mean area of dispersal for passive behaviour was found at the -10m depth (5995.9km²) and the smallest at the deepest depth of -50m (3291.12km²).

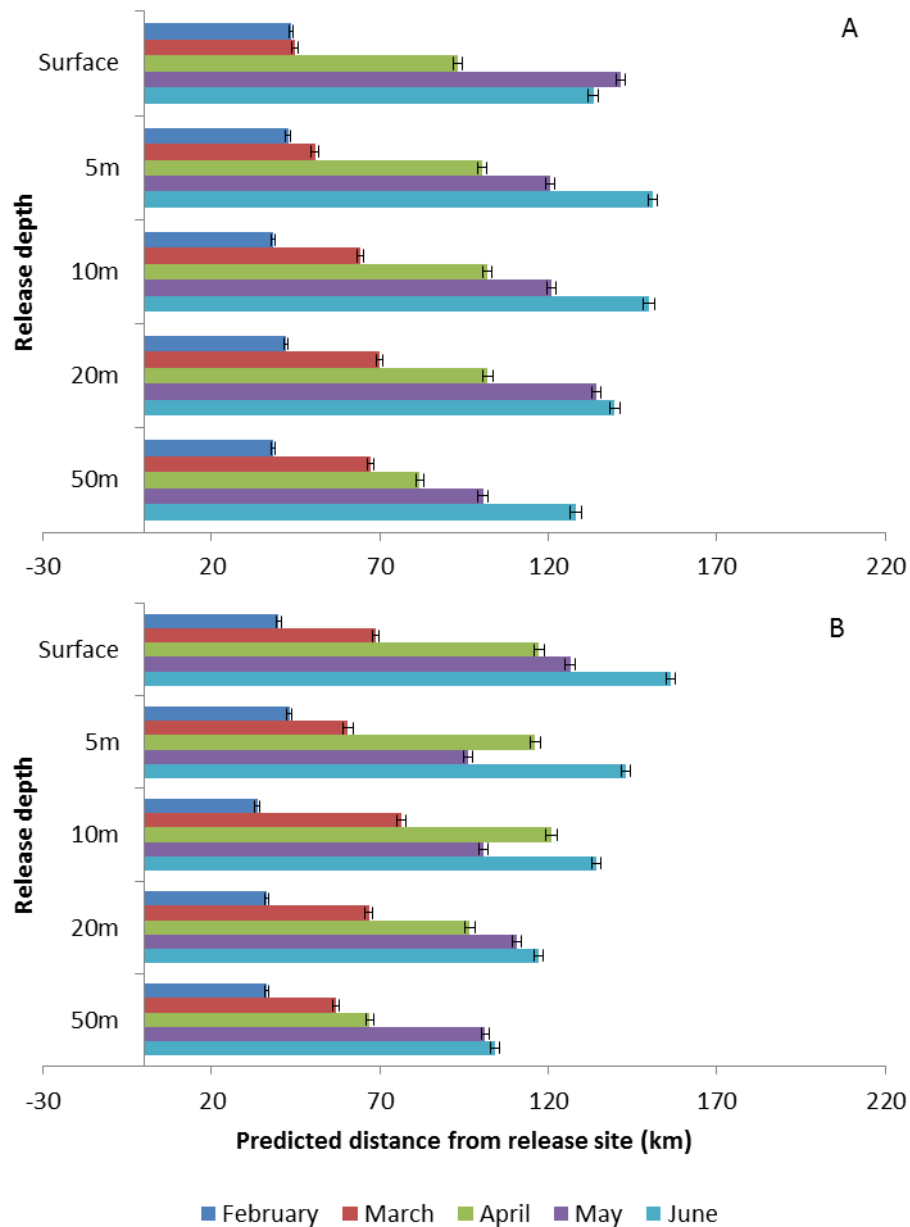


Fig. 3.6 Predicted mean distance of particle travel (km) from release site based on depth for DVM (A) and passive (B) behaviours for offshore locations (\pm SE) found that the lowest mean area of dispersal and lowest mean velocity were observed in particles released at -50m

Potential for retention of particles within historic survey areas

DVM based simulations show an increase in dispersal activity as the spawning season progresses (Fig. 3.7, top). The month of June shows the maximum extent of particle dispersal, with outputs from both Splaugh Rock and IGFS 4 potentially supplying particles to all four historic inshore survey areas. Particles released at the Bar Rocks and Splaugh Rock inshore locations were retained at Youghal and Splaugh Rock respectively for each month of the spawning season, showing evidence of local retention. Input from offshore locations was also highest in June, with dispersal from five different offshore spawning locations reaching historic inshore locations. No particles released from offshore locations during March and April simulations were found to be retained at inshore historic locations, though were present within inshore areas.

Passive behavioural simulation outputs showed that the highest transfers of particles from release sites were observed in April, with 10 different spawning locations potentially distributing particles to three of the four historic inshore larval survey locations (Fig. 3.7, bottom). The DVM simulations indicate that larvae from the Bar Rocks and Splaugh Rock spawning locations could supply particles to the historic egg and larval locations of Youghal and Splaugh Rock throughout the course of the spawning season. Particles from offshore locations predominately ended up in Waterford estuary. In comparison, the passive behaviour simulations suggest that Waterford estuary may act as an area of particle retention through the spawning season (February, May and June). Courtown Harbour received a passive behaviour-based simulated particle input on only three occasions over the spawning season, twice from Rusk No.2 (February and May) and once from the Splaugh Rock (June) location. A dispersal trend dominated by the westward movement of particles along the southern coast was apparent from April to June. In contrast, the presence of simulated particles from the offshore location IGFS 3 at Splaugh Rock supports the idea of larvae potentially travelling in a north-eastern direction.

DVM

Release location/historic site	Waterford estuary					Splaugh Rock					Youghal					Courtown				
Bar Rocks																				
Helvick																				
Fundale																				
Splaugh Rock																				
Rusk No.2																				
IGFS 1																				
IGFS 2																				
IGFS 3																				
IGFS 4																				
Discard 1																				
Discard 2																				
Discard 3																				
Discard 4																				

Passive

Release location/historic site	Waterford estuary					Splaugh Rock					Youghal					Courtown				
Bar Rocks																				
Helvick																				
Fundale																				
Splaugh Rock																				
Rusk No.2																				
IGFS 1																				
IGFS 2																				
IGFS 3																				
IGFS 4																				
Discard 1																				
Discard 2																				
Discard 3																				
Discard 4																				

Fig. 3.7 Predicted sources of larvae for historic inshore sites over different months of simulation (orange = February; yellow = March; purple = April; blue = May; green = June) based on DVM (top) and passive (bottom) behaviours. Simulation of particle dispersal later in the spawning season (May and June) resulted in an increase in the number of individual sources of particles dispersed to historical inshore sites

In contrast to particle/larval release sites where retention was observed in inshore waters, offshore spawning sites located in the Irish Sea showed a progressively northwards movement of particles throughout the course of the spawning season, with results from locations IGFS 1 and Discard 2 suggesting the potential for particles to be distributed as far north as the southern coast of Scotland and the northern coast of Ireland (Fig. 3.8).

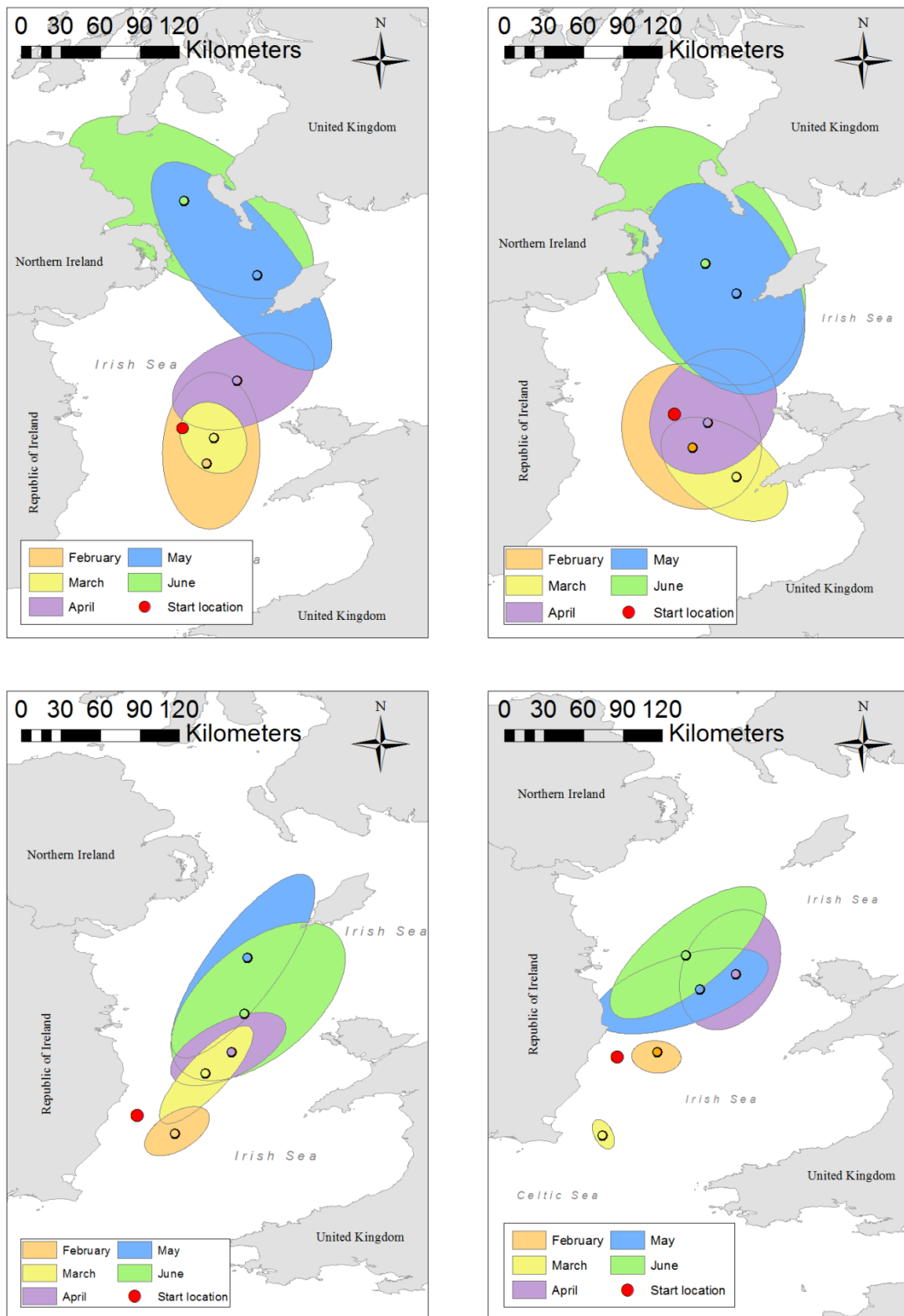


Fig. 3.8 The predicted progressive northwards dispersal of particles from offshore spawning locations Discard 2 (DVM – top, right; passive – top, left) and IGFS 1 (DVM – bottom, right; passive – bottom, left) in the Irish Sea suggests that dispersal may reach as far as the Isle of Man, the north coast of Ireland and the south-west coast of Scotland

PSAT location results

The estimated track of fish 145143 reported in Chapter 5 suggested the presence of a tagged sea bass in offshore waters to the west of Morecambe Bay during the assumed peak period of spawning in May 2016 (output for other PSAT tagged specimens is covered by IGFS 2). DVM simulation output found that particles recorded the furthest mean distance travelled and velocity in May (14.8km at 0.25km/day^{-1}), with June having the lowest (0.53km at 0.01km/day^{-1}) (Fig. 3.9). In contrast, passive behaviour simulations found that June had the highest rate of mean particle velocity (22.4km at 0.37km/day^{-1}), with March recording the lowest (7.7km at 0.13km/day^{-1}) (Fig. 3.10). The smallest area of dispersal was found to occur during April simulations for both behaviours, though the area of dispersal of DVM particles was over five times greater than that of the passive simulation (476.16km^2 in comparison with 90.92km^2). The general trend of particle movement for both DVM and passive behaviour was slightly eastwards, with both behavioural simulations exhibiting high potential for particle retention in nearby inshore areas, particularly in May.

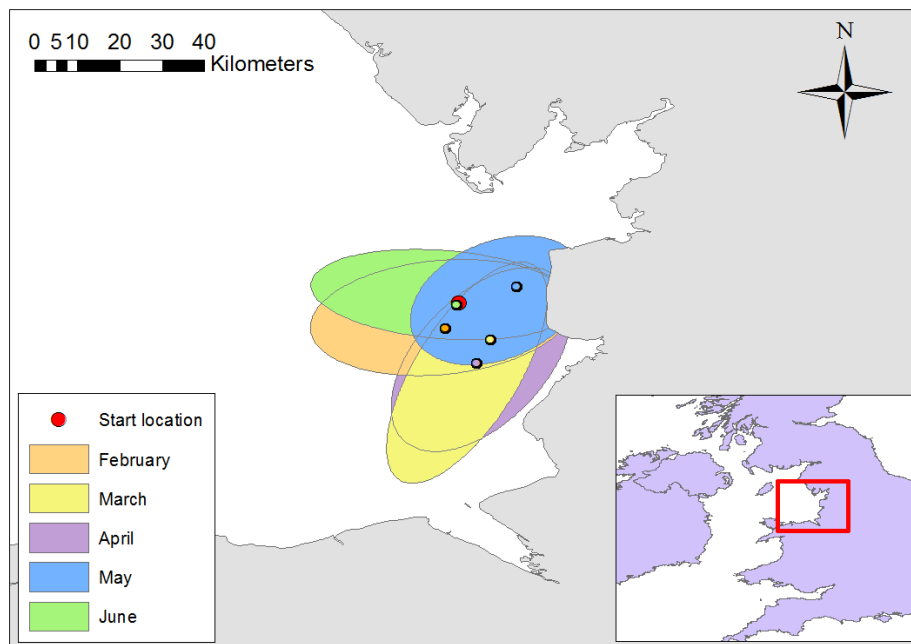


Fig. 3.9 Predicted dispersal of particles from estimated PSAT location based on DVM behaviour

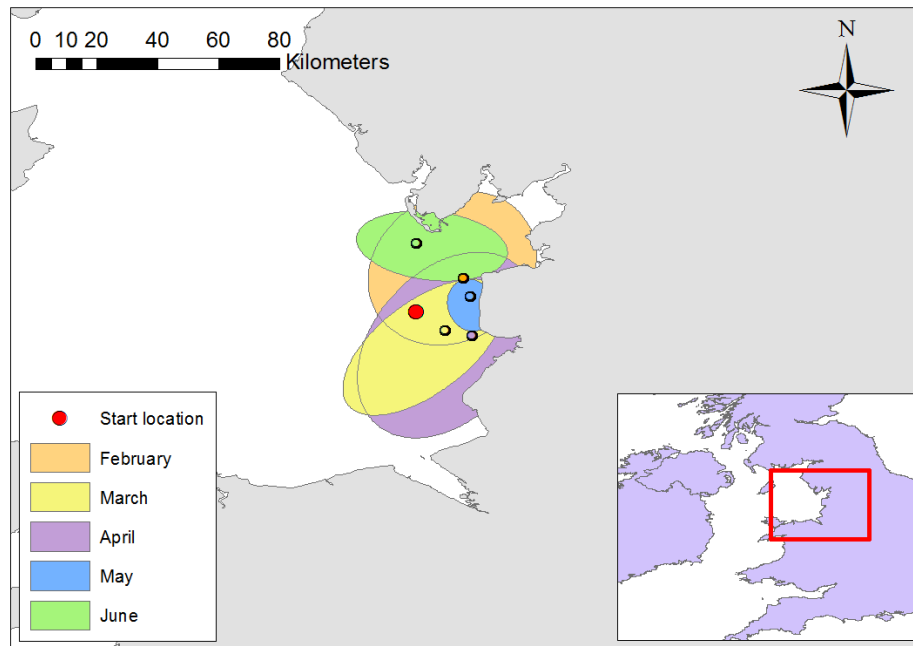


Fig. 3.10 Dispersal of particles from estimated PSAT location based on passive behaviour

Discussion

The use of LTRANS to investigate potential egg and larval dispersal of European sea bass after spawning has provided an insight into how larvae might be transported away from both inshore and offshore putative spawning locations into nursery zones. While the effects of oceanic currents on the swimming ability of larvae were previously thought to be the principal factor affecting dispersal (Harden Jones, 1968), it would appear from simulations of the results of this study suggest that the location and timing of the spawning events may also be highly influential in determining the extent of larval dispersal and, consequently, the distribution of juvenile sea bass.

Temporal and spatial aspects

Pickett and Pawson (1994) suggest that low water temperatures, such as those found at inshore spawning locations in February 2012 (Table 3.1), may limit spawning and/or force

further migration of adult fish into deeper, warmer offshore waters. The extent to which sexually maturing sea bass have to travel to spawn may vary annually, with some winters having a more significant and prolonged impact on inshore water temperatures, such as increased freshwater input and lower air temperatures, than others (Armstrong & Drogou, 2014). The results of the February spawning simulations, irrespective of temperature at the inshore locations, further suggest that particle dispersal is confined to relatively small areas in the early springtime in comparison to other months. This is most likely due to the weak thermal front at the interface between the Celtic Sea and Irish Sea being established at this time of the year, which drives currents along the southern coast (Miller & Christodoulou, 2014; Fernand *et al.*, 2006). At offshore locations, despite water temperature being sufficiently warm to allow spawning to occur, the models show a similar pattern of limited dispersal and low average larval velocities. In contrast, simulations of larval dispersal later in the spring and early summer (April, May and June) suggest the potential for dispersal over greater distances and larger areas, in accordance with the establishment and strengthening of the Celtic Sea front. The increasing water temperatures with the progression of the spawning season may potentially impact on the survivability of larvae, if temperatures were to exceed the upper threshold of 15°C. However, as reported by Jennings & Pawson (1991), sea bass larvae can tolerate higher water temperatures up to 17°C, particularly at later stages of development. Additionally, the establishment of thermal fronts and boundaries, such as the Irish Sea/Celtic Sea front, may also potentially limit dispersal, particularly as the spawning season progresses (Appendix 2.1 to 2.5), though model output for both behaviours resulted in particles transported towards inshore regions across all months. Therefore, these results suggest that the potential dispersal from or retention of particles within a given area, and hence local recruitment, would be strongly influenced by the time of spawning. It also suggests that the extent of the area into which particles may disperse increases as the spawning season progresses.

Particle releases at inshore locations such as Helvick, Bar Rocks and Fundale show dispersal patterns towards and along the southern coast, with particle dispersal typically increasing along the south-west/north-east axis as the spawning season progresses. Previous research on oceanographic processes in the Celtic Sea has found an anti-clockwise circulation with the current on the southern coast of Ireland travelling in a south-westerly direction (Fernand *et al.*, 2006; Bailly du Bios *et al.*, 2002). However, this trend was not observed in June simulations from Bar Rocks and Helvick under passive behaviour conditions (Fig. 3.4, bottom right). The offshore movement of particles observed from these simulations is most likely due to weather forcing effects on particles higher in the water column and contrast the coastal dispersal observed from the corresponding DVM simulation (Appendix 2.6, bottom). The mean depths of the particles on a five-day basis (Appendix 2.10 and 2.11) show that particle depths for DVM behaviour simulations were greater than that for passive scenarios, thereby reducing the potential effect of horizontal weather forcing and resulting in a reduction in offshore dispersal.

Simulations at offshore locations such as those at Discard 1, Discard 3 and IGFS 3 also suggest movement of particles towards inshore zones over the course of the spawning season, evident from the their contribution of particles to historic larval sites (Fig. 3.7). This movement of particles may be possibly attributed to prevailing winds, as identified in the distribution of larvae in Galway Bay (Comerford & Brophy, 2013). In the Irish Sea, however, the prevailing currents/weather would lead to the offshore movement of particles in a northerly direction. It may be inferred from this that larvae spawned in these areas would be naturally carried away from known inshore nursery zones, potentially resulting in reduced recruitment due to high levels of larval mortality. The suggested area of strong particle retention at Splaugh Rock is consistent with the observations of sea bass guides operating within the locality who report large numbers of young sea bass at this location (Jim Hendrick, pers. comm.; Sean Rooney, pers. comm.). Additionally, the simulation output for both

passive and DVM behaviours for particles released in Liverpool Bay indicate a strong likelihood of local retention, suggesting that spawning events occurring within this locality may lead to predominately local recruitment.

While the proposition that larvae are more efficiently transported to nursery areas by sub-surface currents was not supported by the output of the model, it is important to note that this output may not be wholly representative of the behaviour of sea bass larvae in the wild. Model output for both behaviours found that surface released particles at inshore release sites were transported furthest and over the largest area, most likely driven by wind effects at the water's surface (Nielsen *et al.*, 1998). The daily vertical movement of particles throughout the water column attributed to DVM behaviour may have prevented particles from remaining at relatively discrete depths. However, the ability of fish larvae to regulate their depth within the water column, despite currents and turbidity, is well documented (Grioche *et al.*, 2000; Leis, 2006; Huebert, 2008; Duffy-Anderson *et al.*, 2014). It may therefore be possible that sea bass larvae are able to actively regulate their depth to take advantage of accelerated transport pathways to inshore nursery zones and this is not reflected in the model output. However, offshore release of particles found that the -20m release depth, based on DVM behaviour, resulted in the largest dispersal area.

Behavioural component

One of the most noticeable differences in the model outputs between both behavioural types was the magnitude and shape of the area of dispersal. Both overall and split depth simulations exhibit outputs where passive dispersal area is up to double that of DVM. This result has been described in previous particle modelling research, most notably in the larvae of the Caribbean spiny lobster, *Panulirus argus* (Butler *et al.*, 2011) and also in Robins *et al.* (2013). This could be explained by the vertical swimming behaviour of the larvae, as a

method of actively influencing how they are transported. The act of swimming vertically throughout the water column on a daily basis reduces the ability of larvae to swim horizontally, thus reducing overall distance travelled, but may convey other advantages to survival such as avoidance of predators (Ohman, 1990).

Without direct observations of the behaviour of sea bass larvae in the wild, it is difficult to ascertain how they are transported into inshore nursery zones. Such knowledge would be useful for parameterising and ground-truthing the model and therefore achieving more accurate simulation outputs. In particular, behaviour may change over the course of the development of the larvae and therefore the inter-stage developmental behavioural component should possibly be adapted for use on species where this is common (North *et al.*, 2004). An exploratory larval survey in April 2016 recorded no presence of sea bass eggs or larvae in Irish inshore waters or in the Celtic Sea (see Appendix 3.0).

There is also poor understanding currently as to how sea bass larvae select a particular estuary or nursery zone. Atlantic salmon (*Salmo salar*) are renowned for their ability to return to the stream from which they were spawned (Dittman and Quinn, 1996) and homing behaviour has been documented even in seemingly open water fishes such as the Atlantic herring, *Clupea harengus* (Secor, 2015). It is possible that larval sea bass are attracted to and can orientate towards retentive estuarine plumes which bring them into inshore zones, similar to the behaviour of larval Japanese sea bass, *Lateolabrax japonicus* (Secor, 2015). It is also possible that their behaviour is quite random, more similar to the larval dispersal and recruitment into rivers characteristic of the European eel (*Anguilla anguilla*), resulting in them arriving at a suitable habitat to feed and grow by chance. While it is currently unknown which environmental cues, if any, trigger the movement of sea bass larvae into inshore nursery zones (Jennings & Pawson, 1992), likely candidates are differences in salinity, temperatures or the presence of underwater currents and associated ambient noise at the entrance of these nursery habitats/estuaries or combinations of these factors. This behaviour

may potentially have a direct impact on sea bass larval dispersal, with larvae potentially selecting appropriate nursery habitats closer to spawning locations. An additional consideration when interpreting results regarding dispersal from the putative spawning locations to historic inshore larval sites, is that while larvae may not be within the vicinity of nursery zones at the end of the 60-day simulation, such as was observed for March and April model outputs for offshore release sites (based on DVM behaviour), post-larval sea bass have been documented to feed for up to a month in inshore waters before moving into the vicinity of nursery/estuarine zones (Jennings & Pawson, 1992). This further highlights the limitations of the particle model as these larvae may then be recruited on a local scale, with the model thereby underestimating potential recruitment.

Potential implications for recruitment

A lack of knowledge as to where sea bass spawn within Irish waters has resulted in uncertainty regarding the source of juvenile bass frequenting tidal waters. Recent genetic research has suggested that sea bass in Irish waters are part of a larger population stretching across the waters of north-west Europe (see Appendix 4.0; Coscia & Mariana, 2011). This poses a number of issues regarding the management of a stock which moves freely across different jurisdictions and management areas. The data presented here suggest that were spawning to occur either inshore or offshore, or a combination of both, recruitment to Irish nurseries may be plausible. The results presented here, using temporally variable simulations of passive and DVM informed particle transport, are a proxy for larval transport in actuality, and offer suggestions as to the pathways by which larvae are transported to juvenile nursery areas along Ireland's southern and south-eastern coasts. Kennedy and Fitzmaurice (1968; 1972) believed that sea bass spawned in inshore waters, contrary to what has been documented in many studies from the English Channel and Celtic Sea off the

British coast (Jennings & Pawson, 1992; Reynolds *et al.*, 2003; Armstrong & Drogou, 2014). While the findings of this study do estimate that larvae could be retained in inshore after inshore spawning, care should be taken when interpreting these results as the location of sea bass spawning sites within Irish waters is still unknown. It is more likely that spawning may occur offshore, with the model output suggesting that this is a theoretically plausible source of larvae for Irish nurseries.

The extent of larval dispersal inshore is likely to be influenced by the Celtic Sea thermal front, which becomes established during late spring and early summer. The south-westerly flowing currents along the southern Irish coast increase in strength, potentially resulting in larvae from putative release sites such as Fundale, Helvick, Discard 3 and IGFS 3 to reach the coast of Co. Kerry approximately 200km away to the south-west. It is therefore possible that the resultant spawning output from aggregations of sea bass on the south-eastern coast of Ireland may influence recruitment levels of sea bass populations on the south-western and western coast of Ireland. The implications of such findings could suggest that recruitment success of the sea bass population which spawn in Irish waters is not localised and that factors such as exploitation of spawning sea bass at one location may have a direct influence on recruitment at a regional level.

The effects of freshwater output from a number of large rivers, namely the Rivers Slaney, Suir, Nore, Barrow, Blackwater and Lee on the southern Irish coast must also be taken into account as they can influence the timing and location of spawning, depending on the volume of freshwater they discharge into coastal regions. Large volumes of freshwater input during colder winter periods can lower the temperature of coastal waters (Pawson *et al.*, 2007), which may potentially result in a shifting of spawning location or a delay in spawning. Additionally, lower temperatures, such as those in February and March simulations, may result in a delaying of the establishment of coastal currents along the south coast and at St. George's Channel, resulting in larvae being transported over shorter distances and with less

dispersal. If spawning were to occur inshore, it is probable that larvae spawned in close proximity to nursery zones, such as river estuaries, have an increased possibility of local retention due to the presence of local coastal currents and gyres. These hydrological features may also act as important vectors of retention for sea bass larvae in areas separated over large geographical distances away from spawning activity (Robins *et al.*, 2013).

Additionally, the findings presented here also suggest that there could be a potential impact on recruitment of sea bass in Irish waters due to the operation of the sea bass fishery, particularly on the western coast of Britain. Previous tag/recapture studies have recorded migration of sea bass from western inshore regions in Ireland to offshore sites in the eastern Celtic Sea (Pawson *et al.*, 2007). Fahy *et al.* (2000) have suggested that spawning aggregations in the Celtic Sea were a mix of Irish and British sea bass, while annual demersal surveys carried out by the Marine Institute have recorded sea bass being caught 90km off the southern shore of Ireland in November (see Chapter 2). Research from British waters suggests that the majority of spawning takes place offshore and continues through the spawning season (Dando & Demir, 1985; Pawson & Pickett, 1987; Thompson & Harrop, 1987; Jennings & Pawson, 1992). Aggregations of spawning sea bass targeted by the British commercial fishery therefore may contain fish which originated from the Irish population or which may contribute larvae to Irish nursery zones. Further research regarding the location of spawning sites for sea bass in Irish waters is therefore needed to identify and quantify the effect of these sources of sea bass recruitment at a regional and national level.

Previous tagging studies have suggested that movement of adult fish between Ireland and Britain is very low (Pawson *et al.*, 2007). While previous genetic analysis on populations of European sea bass collected in the British and Irish waters had suggested that the Irish stock may be possibly considered a distinct or sub-population (Fritsch *et al.*, 2007), more recent research has shown that this does not appear to be the case (see Appendix 4.0; Coscia & Mariani, 2011). It would appear from some of the particle tracking work presented here that

substantial quantities of larvae from release locations in the Irish Sea and in the proximity of St. George's Channel are likely to be transported in a north-easterly direction, away from potential inshore nursery zones. Dispersal from these simulations found that particles may be transported to areas such as the south-west coast of Scotland and the northern coast of Ireland, suggesting that spawning at these locations may influence recruitment at an international scale, potentially acting as a source of larvae for British sea bass nurseries. The outputs of this particle tracking model would therefore suggest that spawning by sea bass within Irish waters may possibly have an influence on gene flow and recruitment not only on a regional and national level, but also at an international scale.

Conclusions

The results presented here suggest that spawning of sea bass in both inshore and offshore Irish waters may possibly have an influence on recruitment and gene flow over a large geographical area, covering many different areas of management. Particle tracking models provide a useful means to estimate potential pathways and extent of dispersal of spawning fish but may lack the necessary accuracy to account for intrinsic larval behaviours and therefore caution must be taken when interpreting these results. In addition, the contemporary spawning locations of sea bass in Irish waters are still unknown and identification of these areas will produce more accurate simulation output. Nonetheless, it is likely that the dispersal and method by which sea bass are recruited into Irish nurseries, either through inshore or offshore spawning (or a combination), is significantly influenced by the timing and location of spawning events.

Acknowledgements

This research was supported by the Beaufort Marine Research Award in Fish Population Genetics funded by the Irish Government under the Sea Change Programme and by funding received directly from the Marine Institute. The author would like to acknowledge the help offered by members of the Marine Institute and University College Cork during this study.

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Chapter 4

Investigation of inshore site fidelity and the influence of environmental factors on the movement and behaviour patterns of European sea bass, *Dicentrarchus labrax*, on the south coast of Ireland using acoustic telemetry

Abstract

Recent advancements in electronic tag technology has allowed for more accurate investigations into fish behaviour. In Irish waters, the European sea bass (*Dicentrarchus labrax*) is an important recreationally fished species though only basic information about its movements and behaviours has been reported. This study involved the tagging of 44 sea bass on the southern coast of Ireland with acoustic tags and the tracking of their movements from July 2015 to June 2016. The majority (68.5%) of tagged sea bass were detected within 0-5km from their release location only, suggesting little movement between localities and strong evidence of feeding site fidelity. While the majority appeared to remain within relatively discrete areas, travelling over short distances (0-5km), there was also evidence from a small number of tagged sea bass of larger scale geographical movements (>50km) between receiver locations. The amount of time detected specimens spent in the vicinity of receivers decreased from February to June. However, there was an increase in the numbers of individual tagged sea bass present during the same period. Nearly 29% of tagged sea bass were found to be resident within the area of the acoustic array for the entire period of full array deployment (133 days), including the assumed spawning season (February to June), suggesting possible spawning in inshore locations or the possible occurrence of skipped spawning. The consecutive absence periods (>20 days) observed for 21 of the 23 non-resident fish during this same period suggest offshore migration and spawning. For all tagged fish, the most active diurnal periods occurred at dusk and dawn with detection rates lowest during the daylight hours. Detection rates were also found to be influenced by tidal cycles at a number of receiver locations, with two locations at the mouth of estuarine channels recording significantly higher detection rates on ebbing tides. While there was no significant difference in the distances travelled between large and small sea bass, larger specimens were found to travel at a significantly higher speed, undertaking the same journeys in shorter time periods.

Introduction

The European sea bass, *Dicentrarchus labrax*, inhabits marine and estuarine waters around the Irish and British coasts (Pickett & Pawson, 1994). The biology of the species complicates its management as adults are slow to develop, taking between four to seven years to reach sexual maturity (Pawson & Pickett, 1987; Pickett & Pawson, 1994) and can attain a lifespan greater than 20 years (Kennedy & Fitzmaurice, 1972). This slow growth rate makes the species vulnerable to over-exploitation and was considered to be partly responsible for the cessation of the commercial inshore fishery for sea bass in Irish inshore waters in 1990 (Inland Fisheries Ireland, 2014). Today, the fishery is managed nationally as a recreational fishery. Knowledge of the biology and contemporary populations of sea bass in Irish waters is limited.

Previous mark-recapture studies of sea bass around the coasts of Ireland and Britain suggest a complex picture of movement, dispersal and associated behaviours (Kennedy & Fitzmaurice, 1972; Holden & Williams, 1974; Kelley, 1979; Pawson *et al.*, 2007). Adult sea bass in British waters have been found to occupy relatively discrete inshore locations during summer months, with evidence of repeat annual use, while recaptures in offshore waters have revealed migratory routes and spawning areas, particularly in the Celtic Sea and English Channel (Holden & Williams, 1974). Tag returns based on research by Kennedy & Fitzmaurice (1972) suggested that the distribution of sea bass populations in Ireland was essentially local, however, more recent data has suggested that Irish sea bass populations do exhibit large scale movements, with one tagged specimen recaptured 60km off the south-east Irish coast, 3 weeks post-release from an inshore location in the south-west of Ireland (Pawson *et al.*, 2007).

While the data provided by these tag/recapture studies are crucial to understanding fish movements, the use of identification tags in tag/recapture studies offers only limited snapshot into the movement and behaviour of fish, revealing little about daily movements or the

effects of various environmental factors on fish behaviour. In addition, their effectiveness is dependent on the successful recapture and subsequent reporting of the tagged fish (Kennedy & Fitzmaurice, 1972; Holden & Williams, 1974; Pawson *et al.*, 2007). In recent years, the development and use of internal acoustic tags as a method of fish tracking has played a crucial role in progressing biotelemetry for key species with complex behaviours. Sea bass tagged with acoustic transmitters in Cork Harbour on the south coast of Ireland were found to display periods of extended absence from the inshore study area during winter and early spring suggesting that fluctuation of environmental factors on a temporal scale may influence fish presence within the area (Doyle *et al.*, 2017). The use of such technologies may highlight the presence of certain local behaviours, such as extended periods of residency or small home ranges, which could warrant micro-management of inshore stocks.

The ability to record the movements of tagged fish in the vicinity of individual or multiple acoustic receivers allows complex interactions of fish from different areas to be studied in relation to physical and environmental influences. Such information is essential for fishery managers to facilitate the development, maintenance and sustainability of fisheries, particularly of vulnerable stocks. The behaviour of the sea bass in inshore waters is typified by small home ranges and restricted inshore foraging site fidelity, as previously identified by Doyle *et al.* (2017), and therefore suggests that local depletion of the species in Irish waters may occur without effective management of the fishery.

The aim of this study was to investigate sea bass movement, dispersal and behaviour using acoustic telemetry within coastal waters in Ireland. Specifically, an investigation of capture site fidelity and residency of tagged fish within several strategic areas was undertaken. In addition, the interaction of sea bass between different areas while also comparing differences in fish movement and behaviour based on variations in light periods and tidal stages were also analysed. Finally, the seasonal distances and movement behaviours of fish within the study area were also examined.

Materials and methods

Study area

The capture, tagging and release of fish took place along the southern coast of Ireland from November 2014 to April 2016. This coastline is characterized by a mixture of sandy storm beaches and rough, rocky coastline. There are also a number of estuaries and back strands within the survey area, with the largest being the Waterford estuary (which drains the rivers Suir, Nore and Barrow) and Wexford estuary (River Slaney). The study area extends from Youghal, Co. Cork (51.93 N, -7.84 W) in the west to Wexford town in the east (52.34 N, -6.47 W), covering over 120km of coastline (Fig. 4.1 and 4.2).

Specimen acquisition

Specimens of sea bass for tagging were obtained through angling and beach seine netting. Angling, with the help of guides and members of staff from the Marine Institute and University College Cork, was used to target fish from rocky coastlines and estuaries, while seine netting, undertaken by the Marine Institute, was restricted to estuaries and beaches. The seine net used was 100m long x 4m deep, purposely designed by the Marine Institute for the capture of sea bass and constructed by Coastal Nets, UK. The wings of the net were comprised of 42m of 210/30 x 80mm stretched mesh knotted nylon. The cod-end in the centre of the net measured 16m long and was constructed of 210/12 x 20mm stretched mesh knotless nylon which reduced the likelihood of smaller fish escaping and also prevented gilling of larger specimens following the beaching of the net. Once landed, the fish were placed into a large diameter, micro-mesh keep net/cage, which allowed the fish some time to recover prior to surgical insertion of the acoustic transmitter tag.

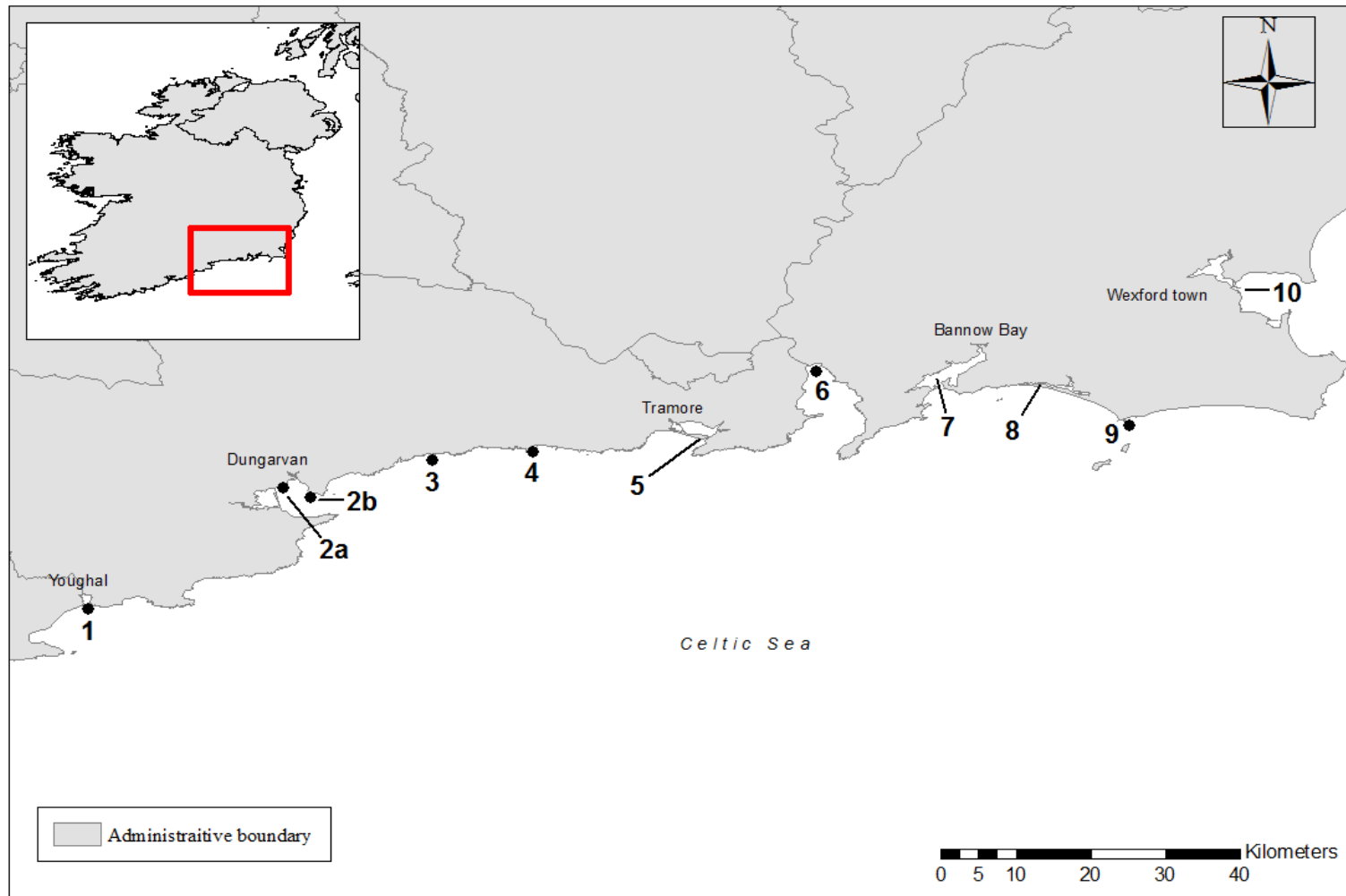


Fig. 4.1 Locations of VR2W receiver deployment (close-ups of locations 5, 7, 8 and 10 in Fig. 4.2) across the 120km study area along the south-east coast of Ireland

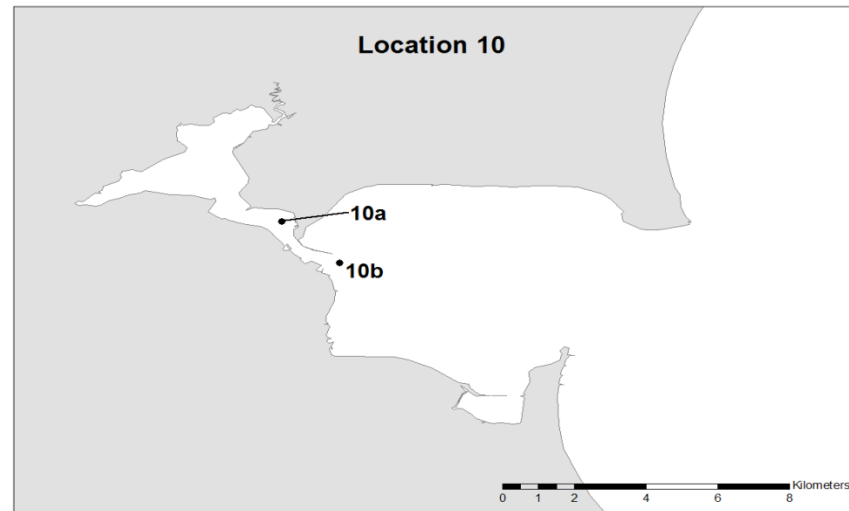
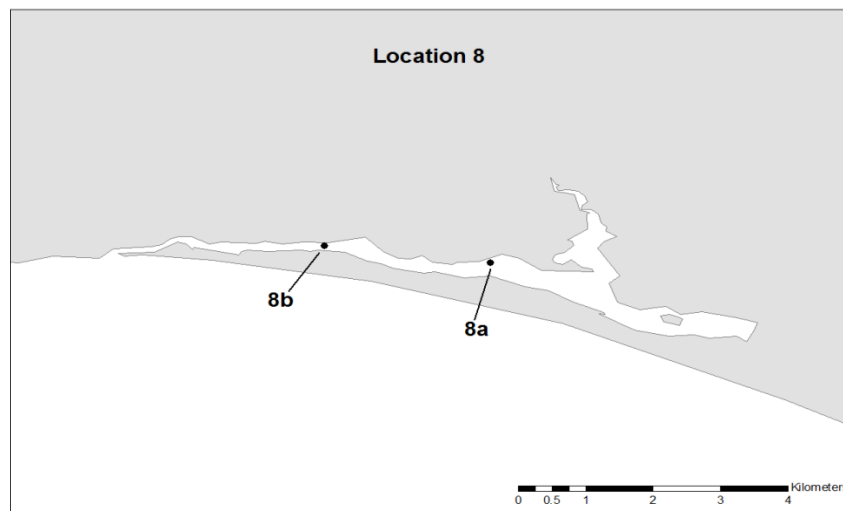
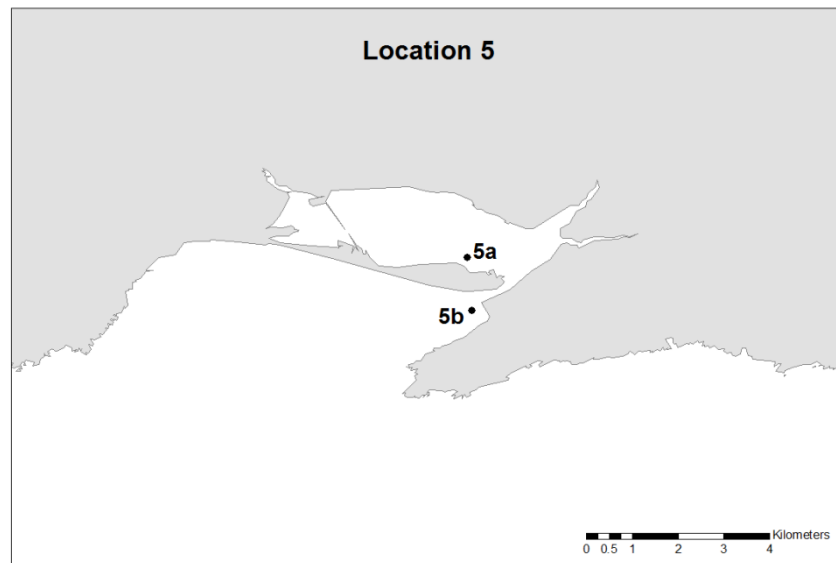


Fig. 4.2 Close up of approximate receiver deployment locations

Surgical insertion of acoustic transmitter tags

Tagged specimens were placed in a holding tank containing a mixture of seawater and 2-phenoxyethanol to induce anaesthesia (approximately 40ml per 80 litres of sea water). Once gill movement was slowed, but still rhythmic, and the fish had lost equilibrium, the sea bass was placed with its ventral side facing upwards on a trough lined with a surgical drape. A hose, connected to a reservoir containing a mixture of seawater and anaesthetic, was placed into the mouth of the fish to ensure a constant supply of water to the gills during tag insertion and maintain the effects of the anaesthetic during the procedure.

The tags used in this study were manufactured by Vemco (Amirix, Nova Scotia, Canada). The tag models used were V9 (9mm diameter, 21mm length, 1.6g mass in air, 145-151dB, ~550 days max batt. life), V13 (13mm diameter, 36mm length, 6g mass in air, 147-153 dB, ~1135 max batt. life) and V16 (16mm diameter, 54mm length, 8.1g mass in air, 150-162dB, ~10 years max batt. life) types. Selection of tag size was based on the physical size of fish, that is, smaller fish (40-45cm) were fitted with V9 tags while larger fish (>50cm) were tagged using V16 tags. Tags were stored individually in sterile bags using ethylene oxide for sterilisation. All fish tagged were deemed to be sexually mature based on length (Pickett & Pawson, 1994; IFI, 2014). Tags were set to ping every 60 to 120 seconds to optimise battery life. Data storage tags were not used due to assumed low return rates in the absence of a large-scale commercial sea fishery operating in Irish waters. A list of tagged fish catch locations is available in Table 4.1.

Insertion of the acoustic tag was made through an incision into the intraperitoneal cavity. The tag was inserted by pushing it through the incision in the direction of the anus to avoid any potential accidental damage to internal organs. The incision was closed with non-absorbable suturing material using a continuous lock suture pattern. The fish was placed into oxygenated water to recover and two T-bar anchor identification tags (Hallprint, Australia) were inserted

into the dorsal musculature of the fish at the base of the primary (spiny) dorsal fin to allow for subsequent identification if recaptured. A small tail fin clip was taken and stored in individual vials of molecular grade ethanol for future genetic analysis. Measurements of total length (from the most anterior point of the fish to the most posterior in centimetres), fork length (from the most anterior point of the fish to the fork of the caudal fin in centimetres) and weight (grams) were taken prior to the fish being released, once swimming strongly.

Tagging procedures undertaken in this study were carried out under licence by the Health Products Regulatory Authority (Licence No.: AE19121/P001) and with approval from the University College Cork's Ethics Committee.

Table 4.1 Catch locations, dates and length/weight measurements for acoustically tagged sea bass in this study

Fish ID	Location of capture	Date of capture	Method	Fork length (cm)	Weight (g)
12888	Location 3	24/03/2016	Angling	51	1450
12899	Location 3	23/03/2016	Netting	44.5	700
26221	Location 3	09/09/2015	Netting	48	1530
12902	2km from Location 8	18/06/2015	Netting	49.5	1690
12907	2km from Location 8	18/06/2015	Angling	47	1400
26220	Location 7	18/06/2015	Angling	47.5	1350
26224	Location 7	11/08/2015	Netting	48.5	1450
26225	Location 7	17/06/2015	Netting	56.5	2800
26236	Location 7	18/06/2015	Angling	51.5	1800
12890	Location 8	19/04/2016	Angling	45	1500
12891	Location 8	19/04/2016	Netting	45.5	600
12894	Location 8	12/11/2015	Angling	53.5	1950
12895	Location 8	17/02/2015	Angling	48	1200
12903	Location 8	04/03/2015	Angling	51.3	1600
12905	Location 8	17/02/2105	Netting	48.5	1600
26207	Location 8	17/02/2015	Angling	45	1900
26208	Location 8	21/04/2016	Netting	65	3600
26210	Location 8	05/11/2014	Angling	45	1600
26213	Location 8	20/11/2014	Angling	48.8	1600
26215	Location 8	21/04/2016	Netting	64.5	3200
26218	Location 8	10/11/2015	Netting	52	2360
26219	Location 8	03/03/2015	Netting	71.5	4479
26222	Location 8	11/11/2015	Netting	61.5	3750
26229	Location 8	17/02/2015	Netting	64.5	3580
26230	Location 8	03/03/2015	Angling	55.5	2100

Fish ID	Location of capture	Date of capture	Method	Fork length (cm)	Weight (g)
26232	Location 8	17/02/2015	Netting	50	1800
26233	Location 8	11/11/2015	Netting	55.5	2100
26235	Location 8	17/02/2015	Angling	53.5	2400
12889	Location 2	15/10/2015	Angling	56.5	1900
12898	Location 2	14/10/2015	Netting	53.5	1900
26234	Location 2	15/10/2015	Angling	65	2600
26217	2km from Location 8	12/08/2015	Angling	51.5	1900
12892	Location 5	15/09/2015	Angling	51	2000
12893	Location 5	31/10/2015	Angling	N/A	N/A
12896	Location 5	12/09/2015	Angling	47.5	1500
12897	Location 5	15/09/2015	Netting	50.5	1900
12901	Location 5	15/09/2015	Netting	52	1680
12904	Location 5	12/09/2015	Netting	51.5	2000
12906	Location 5	15/09/2015	Netting	55	900
26223	Location 5	15/09/2015	Netting	47	1400
26226	Location 5	14/09/2015	Netting	51	2250
26228	Location 5	12/09/2015	Angling	53.5	1750
26237	Location 5	15/09/2015	Angling	57	2200

Monitoring of tagged fish movements

Fish movements were monitored through a series of acoustic receivers placed along the southern and eastern coastlines (Fig. 4.1 and Fig. 4.2). The receivers were placed in areas where sea bass were known to be present (through angling reports) and where tagged fish had been released, therefore increasing the chances of detection. Deployment duration of receivers is available in Table 4.2. A total of 15 Vemco VR2W acoustic receivers were deployed inverted and mounted on temporary mooring ropes or fixed to permanent structures on the sea bed.

Table 4.2 Corresponding locations of receivers on Fig. 4.1 and Fig. 4.2 (*Receiver was lost from mooring but subsequently recovered; days of deployment at specified location approximate)

Location number	Location type	Days of deployment	Date of retrieval
1	Estuarine	421	01/07/2016
2a	Estuarine	398	01/07/2016
2b	Estuarine	307	01/07/2016
3	Rocky coastal	73	01/07/2016
4	Rocky coastal	256	01/07/2016
5a	Estuarine	404	01/07/2016
5b	Estuarine	132	01/07/2016
6	Estuarine	67	01/07/2016
7a	Estuarine	401	01/07/2016
7b	Estuarine	362	01/07/2016
8a	Estuarine	400	01/07/2016
8b	Estuarine	497	01/07/2016
9	Rocky coastal	~182*	01/07/2016
10a	Estuarine	400	01/07/2016
10b	Estuarine	301	01/07/2016

Receivers were deployed in two different types of location: (i) estuarine/lagoon zones; (ii) rocky coastal locations. Receivers located in estuarine/lagoons areas (locations 1, 2, 5, 6, 7, 8, and 10) were deployed in natural physical bottlenecks, for example between sand bars, where fish movement was constrained relative to the main channel and thus the probability of detection was increased. The estimated detection radius of the receivers was 500m approximately (measured through range testing), though interference from background noise sources, such as poor weather conditions or boat traffic, may have reduced this on certain occasions (Kessel *et al.*, 2014). The aim of deploying receivers at rocky coastal locations (locations 3, 4 and 9) was to monitor the movements of fish tagged and released within the immediate area and also to record movements of tagged fish between different estuarine locations (locations 2, 5, 6, 7, 8 and 10) in the study area. Downloading of recorded acoustic data and servicing of the receivers was scheduled for every 2 months, depending on prevailing weather conditions. Winter storms in December 2015 resulted in the temporary loss of one receiver at location 4 which was redeployed in February 2016. The receiver at

location 9 was recovered after its mooring broke approximately 3 months after deployment, however redeployment was not feasible. A receiver was also lost at location 3 during March of 2016, but another was redeployed at this location in late May 2016. The locations of the acoustic receivers presented here are approximate in an effort to protect local stocks from exploitation.

Data analysis

This study used the V-Track package (Campbell *et al.*, 2012) for analysis of fish detections and investigations of residency rates. V-Track is an add-in package designed for use with the R statistical program (R Core Team, 2016) and is highly adaptable, allowing the author to define outputs including summary tables based on detections at individual receivers, detections by fish identification numbers, detection data on a temporal scale and also the generation of a distance matrix to investigate and analyse movement patterns of individual fish between receivers within the study area. Detection data were filtered to identify unknown and false-positive detections, which were subsequently sent to Vemco to be investigated and removed if necessary. Detection data for tagged fish within the 48 hour period post-release was also removed due to the possibility of atypical behaviours as a result of the tagging process (Harasti *et al.*, 2015).

Residency analysis

An assessment of site fidelity was achieved by calculating a residence index (RI). The RI was calculated using the method described in Harasti *et al.* (2015). The value of RI ranged between 0 and 1, with value of 0 indicating no detections on any receivers within the deployed array and a value of 1 representing daily detections within the array. A fish was determined to be resident if the RI value was greater than 0.65 as per Harasti *et al.* (2015). RI

calculations were based on the period of full acoustic array deployment from 19/02/2016 to 30/06/2016 (n=133 days). Sea bass which were tagged and released before this period were deemed to have a total possible period of detection (TPD) of 133 days while a number of specimens had a reduced TPD as they were tagged during this period. The significance of the effect of the loss of receiver 3 from 15/03/2016 to 15/05/2016 on RI values was quantified by calculating the RI for each fish with this period included and also excluded and comparing the results using a Wilcox test. If no significant effect was found then detection data from this period could be included in the analysis. The association between fish length and RI was investigated using a separate Pearson correlation test in R.

Changes in detections across time and due to light and tidal cycles

The investigation of the effects of different light periods and tidal state on fish detections was undertaken to examine behavioural differences at a local level within the study area. This analysis was restricted to the same 133 day period as was used for calculating RI. This study used four light periods: civil dawn, day, civil dusk and night. The civil dawn period occurs when the sun is 6° below the horizon until sunrise. Day time period is defined as the time between dawn and civil dusk - occurring when the sun dips below an angle of 6° below the horizon in the evening. Night occurs during the period between dusk and the next dawn period. Values for light periods were obtained from the US Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). Data for light periods and tidal state (obtained from the Marine Institute: <http://data.marine.ie/Dataset/Details/20955>) were assigned to 10 minute bins to allow for comparison with detection data. Mean detection rates per hour for each individual fish for each light period per day were calculated using the following formula:

$$\frac{N_L}{D_L}$$

where N_L was the number of detections of a fish during a light period on a specific date and D_L is the duration of the light period in hours on the same date.

Mixed effect models, using the “lme4” package in R (Bates *et al.*, 2015), were used to investigate the influence of different tide and light periods on the rate of detections while also analysing the changes in mean detection rates over the duration of full acoustic array deployment. This was undertaken on a receiver-by-receiver basis to investigate differences in fish behaviour at a local scale. Recorded acoustic data was explored and validated as per Zuur *et al.* (2010) while normality of the residuals were assessed via visual inspection of fitted values plotted against the residual value and also via quantile-quantile plots as per Villegas-Ríos *et al.* (2013). The unique acoustic code assigned to each tag (fish.id) was designated as the random effect to account for repeated measures and to avoid pseudoreplication. Detection data was \log_{10} transformed for a more normal distribution. Selection of the most parsimonious model was based on the step-down process outlined in Zuur *et al.* (2009). Model selection was made through comparison of AIC_C values with the best model equaling 0, though in situations where competing models were found to have AIC_C values <2, model averaging was undertaken using the “MuMIn” package (Burnham & Anderson, 2002). The validity of models was checked via assessment of residual plots, quantile-quantile plots and checking the variance of the residuals for each level of the predictor variables as per Harasti *et al.* (2015). The significance of each fixed variable was accounted for by comparing a model including the fixed variable and excluding it using the R “anova” function. The Tukey’s pairwise comparison (as part of the “multcomp” package by Horton *et al.*, 2008) was undertaken for each of the multilevel covariates in the chosen ‘best’ fit model to investigate their relationship.

Swimming distances

The investigation of movement for tagged fish accounted for data recorded in the 12 month period from 01/07/2015 to 30/06/2016. The distances fish travelled were calculated using an inbuilt circuitous distance matrix within the V-Track software with additional waypoints, defined by the author, added to allow for movement around physical features such as headlands and bays (Fig. 4.3). Swimming distance was investigated using 2 different methods: (i) analysis of differences in swimming distances on a temporal scale and (ii) analysis of swimming distance per fish over the course of the entire study. Minimum distance travelled per fish was based on the movement of tagged fish between receiver locations using user-defined way points to allow for the shortest possible swimming route around geographical obstacles, such as headlands and islands, and is achieved via the use of the pre-defined waypoints. Movement and distance data could only be quantified for tagged fish which moved between at least two different receivers throughout the course of the study. The effect of fish length (fork length) on distance covered was analysed using a mixed effect model with “fish.id” treated as a random effect to account for repeated measures. Data were log transformed to improve fit. Model selection and evaluation of the importance of fixed variables was carried out as indicated above for “*Changes in detections across time and due to light and tidal factors*”.

Rate of movement (fish swimming speed)

Rate of movement (ROM) was calculated by V-Track taking the distances between geographical locations of receivers and waypoints and the time taken for tagged fish to travel between them and is given in metres per second (m/s^{-1}). The ROM data was calculated from data over the same period as that of “*Swimming distances*” i.e. the 12 month period from 01/07/2015 to 30/06/2016. The relationship between the mean ROM of individual fish and

corresponding fish FL was analysed using a Pearson correlation (normal distribution of data) in R.

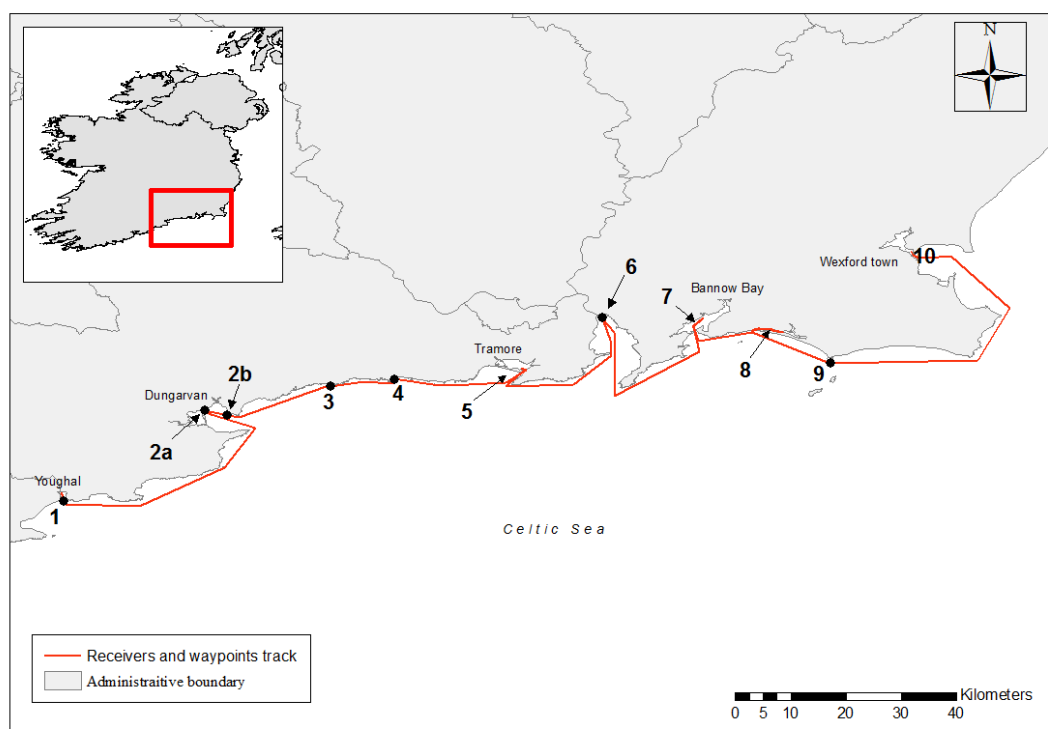


Fig. 4.3 Location of waypoints track used to calculate distances and rate of movement (m/s^{-1}) between receiver locations

Results

A total of 44 fish were acoustically tagged during the course of this study between November 2014 and April 2016 with biological data recorded for 42 fish. A total of 850 hours of effort were required to acquire and tag the specimens. Of the 44 fish acoustically tagged, 38 were tagged and released in estuarine locations with the remaining six tagged and released in areas of rocky coastline. There was no reported recapture of any tagged fish. The average FL and weight of tagged specimens was 52.6cm (SD = 6.2) and 1975.4g (SD = 788.2) respectively, with the size of fish ranging from 45.5cm/600g to 71.5cm/4479g. Identification of individual sex was not possible though all sea bass were assumed to be adults as they were $>42\text{cm}$

(Pawson & Pickett, 1996) while the largest fish were assumed to be females based on observations made by Kennedy & Fitzmaurice (1972).

Residency and fish presence/absence results

Receiver 3 was lost in the period from 15/03/2016 to 15/05/2016 ($n = 61$ days) though its loss was found not to have affected the RI score (paired Wilcoxon test: $p > 0.05$), therefore allowing for the inclusion of detection data from this period. A sea bass was determined to be resident where $RI > 0.65$. Of the 38 fish which were detected 48 hours post tagging, 11 were considered to be resident, with the remaining 27 having RI values below 0.65 (Table 4.3) and thus considered to be non-resident. Of the nine lowest RI values, four belonged to sea bass released at location 7 while four other fish (three from location 8, one from location 5) had a RI of 0 (complete absence) during the period of full array deployment. Of the sea bass with the five highest RI values, two were from location 8, albeit with reduced total period of detection, two were from location 5 and the other fish was from location 2. The low RI values recorded from sea bass released from location 7 (0.08 to 0.02, $n=4$) contrasts with that of location 8 (RI ranging from 1 to 0; $n = 22$) for which a gap period of no detection of only nine days was recorded; this was despite the entrances to both locations being similar and located only 8km apart. In terms of interaction of tagged specimens between sites, no fish from location 7 were detected in location 8, although two sea bass released from location 8 were recorded in location 7. No significant relation was found between RI and FL (Pearson correlation: $r(36) = -0.09$, $p > 0.05$).

Table 4.3 Residence Index (RI) for fish detected during deployment of full acoustic array (TPD: the total period of detection, in days, possible for a tagged fish) (continued overleaf)

Fish ID	FL	K	Closest release location	Location type	Date tagged	Detected post-release	TPD	RI	Resident
26208	52	1.68	8	Estuarine	21/04/2016	Y	69	1	Y
12891	49.5	1.39	8	Estuarine	19/04/2016	Y	70	0.97	Y
12892	47	1.35	5	Estuarine	15/09/2015	Y	133	0.87	Y
26234	47	1.35	2	Estuarine	15/10/2015	Y	133	0.78	Y
12890	48	1.38	8	Estuarine	19/04/2016	Y	70	0.77	Y
26231	N/A	N/A	5	Estuarine	15/09/2015	Y	133	0.77	Y
26232	51.5	1.46	8	Estuarine	17/02/2015	Y	133	0.77	Y
12897	45	1.65	5	Estuarine	15/09/2015	Y	133	0.74	Y
26230	52	1.19	8	Estuarine	03/03/2015	Y	133	0.73	Y
12905	65	1.31	8	Estuarine	17/02/2015	Y	133	0.71	Y
26229	50.5	1.48	8	Estuarine	17/02/2015	Y	133	0.69	Y
26210	71.5	1.23	8	Estuarine	05/11/2014	Y	133	0.59	N
26233	55	0.54	8	Estuarine	11/11/2015	Y	133	0.58	N
12889	44.5	0.79	2	Estuarine	15/10/2015	Y	133	0.57	N
12906	45	1.76	5	Estuarine	15/09/2015	Y	133	0.56	N
26228	47.5	1.40	5	Estuarine	12/09/2015	Y	133	0.53	N
12896	51.5	1.32	5	Estuarine	12/09/2015	Y	133	0.44	N
12904	45	2.09	5	Estuarine	12/09/2015	Y	133	0.44	N
26218	50	1.44	8	Estuarine	10/11/2015	Y	133	0.42	N
26222	53.5	1.24	8	Estuarine	11/11/2015	Y	133	0.42	N
12893	47.5	1.26	5	Estuarine	31/10/2015	Y	133	0.41	N
26223	65	0.95	5	Estuarine	09/15/2015	Y	133	0.4	N
26221	56.5	1.05	3	Rocky	09/09/2015	Y	133	0.39	N
26207	64.5	1.19	8	Estuarine	17/02/2015	Y	133	0.38	N
12898	45.5	0.64	2	Estuarine	14/10/2015	Y	133	0.32	N
12895	56.5	1.55	8	Estuarine	17/02/2015	Y	133	0.3	N
12894	48.5	1.27	8	Estuarine	12/11/2015	Y	133	0.26	N
26215	64.5	1.33	8	Estuarine	21/04/2016	Y	133	0.26	N
26213	61.5	1.61	8	Estuarine	20/11/2014	Y	133	0.11	N
26224	51.5	1.39	7	Estuarine	11/08/2015	Y	133	0.08	N
26236	53.5	1.14	7	Estuarine	18/06/2015	Y	133	0.06	N
12888	51	1.09	3	Rocky	24/03/2016	Y	133	0.05	N
26220	53.5	1.57	7	Estuarine	18/06/2015	Y	133	0.02	N
26225	51	1.51	7	Estuarine	17/06/2015	Y	133	0.02	N
12901	48	1.09	5	Estuarine	15/09/2015	Y	133	0	N
12903	48.5	1.40	8	Estuarine	04/03/2015	Y	133	0	N
26219	55.5	1.23	8	Estuarine	03/03/2015	Y	133	0	N
26235	51	1.70	8	Estuarine	17/02/2015	Y	133	0	N
12899	53.5	1.27	3	Rocky	23/03/2016	N	133	0	N
12902	51.3	1.19	8	Rocky	18/06/2015	N	133	0	N
12907	48.8	1.38	8	Rocky	18/06/2015	N	133	0	N

Fish ID	FL	K	Closest release location	Location type	Date tagged	Detected post-release	TPD	RI	Resident
26217	55.5	1.23	8	Rocky	12/08/2015	N	133	0	N
26226	N/A	N/A	5	Estuarine	14/09/2015	N	133	0	N
26237	57	1.19	5	Estuarine	15/09/2015	N	133	0	N

Fish 12894 and 26222 were all last recorded on receiver 8a, having being confirmed passing receiver 8b in the lower estuary during late May, suggesting that they remained present in the upper reaches of location 8 during June. The additional days of potential presence of fish 12894 and 26222 (days when no detections were recorded in receiver 8a) did not increase their respective residence indexes above the 65% threshold (increasing potentially from 0.26 to 0.285 and 0.42 to 0.61 respectively).

Tagged fish absence during study period

During the 12 month duration of the study, a varying number of tagged fish were detected on a monthly basis. The ratio of the number of tagged fish detected to tagged fish released over this period varied between 0.36 (January and February) to 0.72 (June) per month (mean = 0.57; SD = 0.13) (Fig. 4.4).

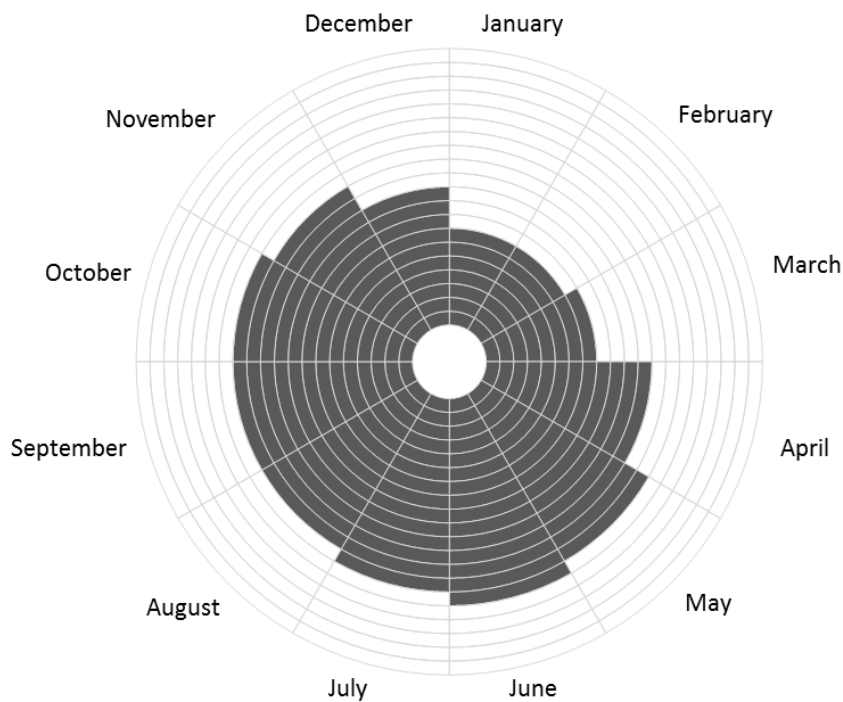


Fig. 4.4 Variation in the percentage of tagged fish detected in relation to numbers of tagged fish released over the duration of the study (each within segment block = 5%). Absence of tagged sea bass was highest during the winter months (December to March) with fish returning from April onwards through to the end of the study period in June

Prior to the period of full acoustic array deployment, a number of fish ($n=31$) had been tagged and detected post-release in the autumn and early winter of 2015. Of these 31 fish, 18 were recorded being absent for a period greater than 30 consecutive days when taking into account an initial absence leave date between September 2015 and February 2016 inclusively (Mean = 130 days, SD = 56.4) (Table 4.4). Of the remaining 13 fish, four had left the detection area of the acoustic array and had failed to be detected again whilst the other nine remained inshore during the same period. When restricted to the period of full acoustic receiver deployment (February 19th to June 30th 2016), the longest consecutive absence periods for non-resident fish ($n = 23$) ranged between 9 and 110 days (mean = 56.7; SD = 29.2) with 21 of the 23 fish having consecutive absence periods over 20 days long, while resident fish were found to be absent for between one and 10 days consecutively (mean = 5.9;

SD = 2.6) during the same period. Fish 26213 was tagged and released on 20/11/2014 though no acoustic receivers were deployed at this stage. The first detection of this fish by a receiver was on 23/08/2015, over 272 days later.

Table 4.4 Tagged fish presence/absence over winter/spring period 2015/2016

Fish.ID	Leave	Leave	Return	No. of days	Leave location	Return location	FL
26225	Yes	11/09/2015	07/06/2016	240	Youghal	Waterford estuary	51
26207	Yes	13/07/2015	22/02/2016	224	Cullinstown	Cullinstown	64.5
26224	Yes	09/10/2015	12/05/2016	214	Bannow Bay	Bannow Bay	51.5
26221	Yes	09/09/2015	04/03/2016	177	Ballydowane	Ballydowane	56.5
12898	Yes	24/10/2015	02/04/2016	161	Dungarvan Bay	Dungarvan Bay	45.5
12895	Yes	17/11/2015	21/04/2016	156	Cullinstown	Cullinstown	56.5
26223	Yes	08/11/2015	11/04/2016	154	Tramore Bay	Boatstrand	65
12896	Yes	17/11/2015	02/04/2016	137	Tramore Bay	Tramore Bay	51.5
26222	Yes	28/11/2015	06/04/2016	130	Cullinstown	Cullinstown	53.5
26210	Yes	18/12/2015	12/04/2016	116	Cullinstown	Cullinstown	71.5
26233	Yes	25/12/2015	13/04/2016	110	Cullinstown	Cullinstown	55
12894	Yes	05/02/2016	24/05/2015	109	Cullinstown	Cullinstown	48.5
26213	Yes	04/12/2015	17/03/2016	94	Youghal	Youghal	61.5
12904	Yes	06/02/2016	01/05/2016	85	Dungarvan Bay	Tramore Bay	45
26229	Yes	06/12/2015	24/02/2016	80	Bannow Bay	Cullinstown	50.5
12906	Yes	11/01/2016	13/03/2016	62	Tramore Bay	Tramore Bay	45
26218	Yes	10/11/2015	09/01/2016	60	Cullinstown	Cullinstown	50
12893	Yes	27/01/2016	03/05/2016	38	Tramore Bay	Tramore Bay	47.5
12901	Yes	30/12/2015	No		Tramore Bay		48
12903	Yes	19/10/2015	No		Cullinstown		48.5
26219	Yes	11/06/2015	No		Cullinstown		55.5
26235	Yes	11/04/2015	No		Cullinstown		51
12889	No				Dungarvan Bay		44.5
12892	No				Tramore Bay		47
12897	No				Tramore Bay		45
12905	No				Cullinstown		65
26228	No				Tramore Bay		47.5
26230	No				Cullinstown		50
26231	No				Tramore Bay		56
26232	No				Cullinstown		51.5
26234	No				Dungarvan Bay		47

Variations in the presence of fish at the different locations showed an increase in fish presence in May and June, particularly at locations 2, 5 and 8 (Fig. 4.5 and Fig. 4.6). No fish from location 7 were recorded present in their release locality from December through to April. Only one local fish was recorded as being present at location 2 from December to the end of March, while the number of local-origin fish detected at location 5 during March was four (33.3%), with 12 fish having being released in this location up to that point. At location 8, only five fish out of a possible 15 (33.3%) released were documented during December and February though this increased to 15 fish out of a possible 19 (79%) during May.

Additionally, all receiver locations, with the exception of locations 8 and 9, recorded migrant tagged fish which had originally been released at other inshore sites. The highest numbers of migrant tagged fish were recorded on receivers at location 1 and 2 with migrants originating from three other release locations. Locations 3, 4 and 5 detected migrant fish from two other origins while locations 6 and 10 only recorded a migrant from one other release location. Fish released from locations 3, 5, 7 and 8 were detected at three other receiver locations within the study area, while those released originally from location 2 were only found at one other location (location 5).



Fig. 4.5 Variation in presence of tagged fish from different release locations at acoustic receiver locations 1 to 6 over 12 month duration (each block within segment = 1 fish; numbers in parentheses = number of fish released at that corresponding location up to the respective month). Location 2 and 5 both saw an increase in tagged fish presence from April to June while locations 3, 4 and 6 reported sporadic presence over the study. While no sea bass were tagged at location 1, migrant tagged fish from three other locations were all detected. One fish tagged at location 2 appears to have over-wintered near location 5 prior to returning to its original release site again in April



Fig. 4.6 Variation in presence of tagged fish from different release locations at acoustic receiver locations 7 to 10 over 12 month duration (each block within segment = 1 fish; numbers in parentheses = number of fish released at that corresponding location up to the respective month). Location 7 recorded no tagged sea bass presence from January to April whereas a number of tagged fish over-wintered in location 8 though no tagged migrants from other areas were recorded there

Temporal, tidal and light influences by receiver locations

Mixed model selection for analysis of tidal, light and month effects at each separate receiver were selected using AICc criteria (Table 4.5). There were notable differences between the effects of tide, light and time on the number of detections per hour across nine of the locations where sufficient data were available (Table 4.6). The effects of these variables on mean detection rates are displayed in Table 4.6 though Table 4.8. A sufficient number of detections over time were recorded by receivers 1, 2a, 2b, 3, 5a, 5b, 7b, 8a and 8b and therefore could be analysed. The results for model selection based on AICc criteria with respect to resident fish only and their corresponding results are displayed in Table 4.10 to Table 4.14.

Table 4.5 The five ‘best’ model candidates, based on AICc, for LMER analysis of tide, light and month effects on detections/hour⁻¹ for all tagged fish

Location	Model	df	AIC	AICc	Model weight	Location	Model	df	AIC	AICc	Model weight
1	~ light + month	7	40.6	0.0	0.51	5b	~ tide + light + month	11	-139.1	0.0	0.98
	~ tide + light	7	41.4	0.9	0.33		~ light + month	10	-131.2	8.0	0.018
	~ tide + light + month	8	43.0	2.5	0.15		~ tide + light	7	-128.2	11.0	<0.001
	~ NULL	3	49.7	9.1	<0.001		~ tide + month	8	4.5	143.6	<0.001
	~ tide + month	5	51.5	10.9	<0.001		~ NULL	3	11.0	150.2	<0.001
2a	~ light + month	10	-117.7	0.0	0.78	7b	~ light + month	7	1.2	0.0	0.62
	~ tide + light + month	11	-115.6	2.1	0.25		~ tide + light	7	3.0	1.8	0.25
	~ tide + light	7	-112.2	5.6	0.04		~ tide + light + month	8	4.4	3.2	0.13
	~ tide + month	8	96.6	214.3	<0.001		~ NULL	3	14.2	13.0	<0.001
	~ NULL	3	98.5	216.2	<0.001		~ tide + month	5	19.4	18.2	<0.001
2b	~ tide + light + month	11	48.3	0.0	1	8a	~ light + month	10	-509.1	0.0	0.7
	~ tide + light	10	63.4	15.1	<0.001		~ tide + light + month	11	-507.4	1.7	0.3
	~ light + month	7	63.7	15.4	<0.001		~ tide + light	7	-484.5	24.6	<0.001
	~ tide + month	8	193.0	144.7	<0.001		~ tide + month	8	412.8	921.9	<0.001
	~ NULL	3	214.6	166.3	<0.001		~ NULL	3	467.1	976.2	<0.001
3	~ light + month	7	40.6	0.0	0.51	8b	~ tide + light + month	11	365.3	0.0	0.56
	~ tide + light	7	41.4	0.9	0.33		~ light + month	10	365.7	0.5	0.44
	~ tide + light + month	8	43.0	2.5	0.14		~ tide + light	7	419.2	53.9	<0.001
	~ NULL	3	49.7	9.1	0.005		~ tide + month	8	1199.7	834.5	<0.001
	~ tide + month	5	51.5	10.9	0.002		~ NULL	3	1255.1	889.9	<0.001
5a	~ tide + light + month	11	-410.0	0.0	0.937						
	~ light + month	10	-404.6	5.4	0.063						
	~ tide + light	7	-184.1	225.9	<0.001						
	~ tide + month	8	351.5	761.5	<0.001						
	~ NULL	3	444.3	854.3							

Table 4.6 Estimated intercepts for fixed effects in models predicting no. of detections/hour⁻¹ and whether tide, light and month differ significantly at that receiver (\pm standard error in parentheses)

Receiver	Type	Model intercept	Tide	Month	Light period
1	Estuary	0.52 (0.19) *	No	No	Yes
2a	Estuary	0.54 (0.09) ***	No	Yes	Yes
2b	Estuary	0.61 (0.10) ***	Yes	Yes	Yes
3	Rock	0.66 (0.15) ***	No	No	Yes
5a	Estuary	0.92 (0.04) ***	Yes	Yes	Yes
5b	Estuary	1.17 (0.08) ***	Yes	Yes	Yes
7b	Estuary	0.54 (0.14) ***	No	Yes	Yes
8a	Estuary	0.65 (0.12) ***	No	Yes	Yes
8b	Estuary	1.03 (0.05) ***	No	Yes	Yes

Table 4.7 Estimated intercepts and z-values (in parentheses) comparing detections/hour⁻¹ to tidal stages (p<0.05 *, p<0.001 ***, no significance = n/s)

Receiver location/tide	1	2a	2b	3	5a	5b	7b	8a	8b
Flooding - ebbing	n/s	n/s	-0.11 *** (-4.2)	n/s	0.03 * (2.73)	-0.06 * (-3.2)	n/s	n/s	n/s

Table 4.8 Estimated intercepts and z-values (in parentheses) comparing detections/hour⁻¹ over months (p<0.05 *, p<0.001 ***, no significance = n/s)

Receiver location	Mar-Feb	Apr-Feb	May-Feb	June-Feb	Apr-Mar	May-Mar	June-Mar	May-Apr	June-Apr	June-May
1	n/s									
2a	n/s	n/s	n/s	n/s	0.16 * (2.76)	n/s	n/s	n/s	n/s	n/s
2b	n/s	0.31 * (3.63)	0.28 *** (3.89)	0.27 *** (4.21)	n/s	0.18 * (2.82)	0.16 * (3.09)	n/s	n/s	n/s
3	n/s									
5a	n/s	n/s	-0.19 *** (-6.03)	-0.21 *** (-6.75)	-0.15 *** (-7.46)	-0.26 *** (-14.12)	-0.28 *** (-15.21)	-0.11 *** (-6.3)	-0.13 *** (-7.41)	n/s
5b	-0.29 * (-3.7)	-0.29 *** (-4.06)	-0.22 * (-3.29)	-0.26 *** (-4.02)	n/s	n/s	n/s	n/s	n/s	n/s
7b	n/s									
8a	n/s	n/s	n/s	n/s	n/s	n/s	n/s	-0.04 * (-2.89)	-0.08 *** (-5.25)	-0.04 * (-3.12)
8b	n/s	-0.09 * (-3.294)	-0.12 *** (-4.24)	-0.21 *** (-6.87)	n/s	n/s	-0.14 *** (-5.66)	n/s	-0.12 *** (-6.45)	-0.09 *** (-4.95)

Table 4.9 Estimated intercepts and z-values (in parentheses) comparing detections/hour⁻¹ over different light periods (Note: p<0.05 *, p<0.001 ***, no significance = n/s)

Receiver location	Day-Dawn	Dusk-Dawn	Night-Dawn	Dusk-Day	Night-Day	Night-Dusk
1	n/s	n/s	n/s	n/s	0.22 * (2.66)	n/s
2a	-0.49 *** (-10.63)	n/s	-0.39 *** (-8.37)	0.57 *** (14.12)	0.09 *** (4.04)	-0.47 *** (-11.44)
2b	-0.53 *** (-9.59)	n/s	-0.45 *** (-7.68)	0.59 *** (10.79)	0.08 * (2.77)	-0.51 *** (-8.84)
3	n/s	n/s	-0.43 * (-3.07)	n/s	n/s	-0.67 * (-3.15)
5a	-0.61 *** (-22.19)	0.14 * (3.51)	-0.50 *** (-17.45)	0.75 *** (24.38)	0.11 *** (8.6)	-0.64 *** (-20.42)
5b	-0.66 *** (-13.44)	n/s	-0.68 *** (-9.72)	0.39 * (2.86)	n/s	-0.41 * (-2.88)
7b	-0.32 * (-2.68)	0.46 * (2.82)	-0.41 * (-2.85)	0.79 *** (6.31)	n/s	-0.88 *** (-5.86)
8a	-0.62 *** (-25.71)	n/s	-0.47 *** (-19.12)	0.58 *** (26.80)	0.15 *** (12.81)	-0.44 *** (-19.65)
8b	-0.59 *** (-26.82)	n/s	-0.48 *** (-21.04)	0.54 *** (21.84)	0.01 *** (7.97)	-0.43 *** (-17.05)

Table 4.10 The five ‘best’ model candidates based on AICc for LMER analysis of tide, light and month effects on detections/hour⁻¹ for resident fish only

Location	Model	df	AIC	AICc	Model weight	Location	Model	df	AIC	AICc	Model weight
5a	~ tide + month	8	496.2	0.0	0.939	8a	~ tide + month	8	975.3	0.0	0.473
	~ tide + light + month	11	501.7	5.5	0.061		~ tide + light	7	975.6	0.3	0.416
	~ tide + light	7	536.3	40.1	<0.001		~ tide + light + month	11	979.3	4.0	0.064
	~ NULL	3	595.7	99.5	<0.001		~ NULL	3	980.1	4.8	0.044
	~ light + month	10	595.9	99.8	<0.001		~ light + month	10	985.5	10.1	0.003
5b	~ tide + month	8	50.4	0.0	0.589	8b	~ tide + month	8	435.3	0.0	0.733
	~ NULL	3	51.4	1.0	0.359		~ tide + light + month	11	437.4	2.2	0.249
	~ tide + light	7	56.5	6.0	0.029		~ light + month	7	443.8	8.5	0.010
	~ light + month	10	57.7	7.3	0.016		~ tide + light	10	444.6	9.4	0.006
	~ tide + light + month	11	59.0	8.6	0.008		~ NULL	3	449.5	14.2	<0.001

Table 4.11 Estimated intercepts for fixed effects in models predicting no. of detections/hour⁻¹ and whether tide, light and month differ significantly at that receiver based on data from resident fish only (\pm standard error in parentheses)

Receiver	Type	Model intercept	Tide	Month	Light period
5a	Estuary	1.01 *** (0.06)	Yes	Yes	n/s
5b	Estuary	1.14 *** (0.15)	n/s	n/s	n/s
8a	Estuary	1.36 *** (0.12)	Yes	n/s	n/s
8b	Estuary	1.23 *** (0.03)	Yes	Yes	n/s

Table 4.12 Estimated intercepts and z-values (in parentheses) comparing detections/hour⁻¹ to tidal stages (Note: p<0.05 *, p<0.001 ***, no significance = n/s)

Receiver location/tide	5a	5b	8a	8b
Flooding - ebbing	0.46 *** (10.43)	n/s	-0.13 * (-2.86)	0.09 * (3.06)

Table 4.13 Estimated intercepts and z-values (in parentheses) comparing detections/hour⁻¹ across months for resident fish only (Note: p<0.05 *, p<0.001 ***, no significance = n/s)

Receiver location	Mar-Feb	Feb-Apr	Feb-May	June-Feb	Mar-Apr	May-Mar	Mar-June	May-Apr	June-Apr	May-June
5a	n/s	n/s	0.35 * (3.77)	-0.33 * (-3.42)	0.21 * (3.29)	-0.35 *** (-6.15)	0.33 *** (5.32)	n/s	n/s	n/s
5b	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s
8a	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s
8b	n/s	-0.22 * (-3.22)	-0.20 * (-3.04)	n/s	n/s	n/s	n/s	n/s	n/s	n/s

Table 4.14 Estimated intercepts and z-values (in parentheses) comparing detections/hour⁻¹ over different light periods for resident fish only (Note: p<0.05 *, p<0.001 ***, no significance = n/s)

Receiver location	Day-Dawn	Dusk-Dawn	Night-Dawn	Dusk-Day	Night-Day	Night-Dusk
5a	n/s	n/s	n/s	n/s	n/s	n/s
5b	n/s	n/s	n/s	n/s	n/s	n/s
8a	n/s	n/s	n/s	n/s	n/s	n/s
8b	n/s	n/s	n/s	n/s	n/s	n/s

Tidal influence was significant at receiver 2b where more detections/hour⁻¹ were recorded during ebbing tides (intercept: -0.11, z-value = -4.2, p<0.001). There was a significantly higher detection rate also on the ebbing tide found at receiver 5b (intercept: -0.06, z-value = -3.2, p<0.05) but receiver 5a recorded a significantly higher detection rate (intercept: 0.03, z-value = 2.73, p<0.05) on the flooding tide. However, it was found that when restricted to resident sea bass at location 5 only (n=3), there was significantly higher detection rate on the ebbing tide at 5a (intercept: 0.46, z-value = 10.43, p<0.001). It can be therefore inferred, that the general pattern of movement for all tagged sea bass at location 5 was to move into the back strand via the main channel and remain in the vicinity of the 5a receiver for the majority of the flooding tide. At the beginning of the ebbing tide, resident sea bass were more likely to remain in the vicinity of receiver 5a while other sea bass spent the majority of the ebbing tide in the vicinity of the 5b receiver in the mouth of the channel. Resident fish at location 8 (n=7) also had significantly higher detection rates during ebbing tides at receiver 8b (intercept: 0.09, z-value = 3.06, p<0.05) in the lower section of the estuary in contrast to the significantly higher rate observed during flooding tides at receiver 8a (intercept: -0.13, z-value = -2.86, p<0.05) further up the channel.

Changes in detection rates over time (months) were also evident at seven of the nine receivers. Receiver 2a recorded a significant increase in detection rates during April (intercept: 0.16, z-value = 2.76, p<0.05), but no significant differences were found at other times. While the detection rate at receiver 2b did increase throughout the study period, the month on month increase was not deemed to be significant. Detections/hour⁻¹ at receiver 5a decreased significantly on consecutive months from March through until May. Receiver 5b also recorded a similar pattern in detection rates to 5a, decreasing slowly from March to the end of the study period in June. The only significant decrease in the detection rate at receiver 5b noted was between February and March (intercept: -0.29, z-value = -3.7, p<0.05), though in resident sea bass only, while a significantly higher detection rate was observed at receiver

5a during February than at either April or May (intercept: -0.22, z-value: -3.22, $p < 0.05$; intercept: -0.2, z-value: -3.04, $p < 0.05$ respectively). Receivers 8a and 8b also recorded a decreasing trend in detections/hour⁻¹, with 8a recording a significant decrease from April to May (intercept: -0.04, z-value: -2.89, $p < 0.05$) and from May to June (intercept: -0.04, z-value: -3.12, $p < 0.05$) while at 8b, the only significant decrease in detections occurred between May and June (intercept: -0.09, z-value: -4.95, $p < 0.001$).

Differences between light periods were the most consistent influence across all receivers with respect to total tagged sea bass. A total of six of the nine receivers (2a, 2b, 3, 5a, 7b and 8a) recorded the highest detections/hour⁻¹ at dusk while dawn was the most active period at 5b and 8b. At receiver 1, most activity was recorded at night. Day periods were found to possess the lowest detection rates in 7 of the 9 receivers (1, 2a, 2b, 3, 5a, 8a and 8b), while there was no significant differences between night and day detection rates at receivers 5b and 7b. In contrast, light period was found to be not significant for resident sea bass specifically at any receiver location.

Swimming distances and rate of movement (ROM)

A total of 1977 journeys were recorded across the receiver network between July 1st 2015 and June 30th 2016. The mean distance travelled for tagged sea bass was 1.38km (SD = 4.21km) with the longest journey found to be 104.5km over 270.3 days and the shortest journey recorded between receivers 8a and 8b at 0.9km. Of the 20 longest journeys recorded, six were made by sea bass released from rocky shores ($n=2$) with the remaining 14 from estuarine released fish ($n=7$). Analysis of individual journeys undertaken by sea bass released from different locations showed that fish released in the locality of receiver location 3 had the highest mean distance covered per journey at 8.08km (SD = 11.55km), while sea bass released in the estuary at location 8 had the lowest at 0.975km (SD = 1.59km).

The highest mean distance travelled per month was observed in September (Table 4.15) with 32.25km per detected fish (n=8), while the lowest recorded mean distance travelled was found in January at 5.28km per detected fish (n=7). The average mean minimum distance travelled per sea bass/month⁻¹ over the 12 month period was 18.68km (SD = 21.3). Model selection for distance covered (Table 4.16) found that ‘month’ had the highest model weight of 0.73 with ‘fork length’ having a model weight of 0.27, therefore showing that the ‘month’ model offered the best explanation of the differences in sea bass travel distances. The results showed that smaller sea bass were found to travel greater distances than larger specimens, though this was not significant (Fig. 4.7). There was however a significant difference in distance travelled across different months with February (intercept: 7.36, estimate: 0.23, p<0.05) and December (intercept: 7.36, estimate: 0.2, p<0.001) recording significantly more distance travelled than other months.

Table 4.15 Mean distance travelled for all tagged fish on a monthly basis for the 12 month period of 01/07/2015 to 30/06/2016

Month	No. of fish	Mean distance per fish (km)	SD
July 2015	10	22.49	39.39
August 2015	7	15.01	8.64
September 2015	8	32.25	31.05
October 2015	9	22.79	15.75
November 2015	11	8.08	7.15
December 2015	7	14.54	8.22
January 2016	7	5.28	3.58
February 2016	7	15.70	27.19
March 2016	12	15.53	14.02
April 2016	20	15.31	16.55
May 2016	25	20.59	20.04
June 2016	23	25.68	20.89

Table 4.16 The four ‘best’ model candidates based on AICc for LMER analysis of distance travelled for tagged fish

Model	df	AIC	AICc	Model weight
~ month	14	646.2	0.0	0.73
~fork length + month	15	648.2	2.0	0.27
~ NULL	3	699.5	53.2	<0.001
~ fork length	4	701.4	55.2	<0.001

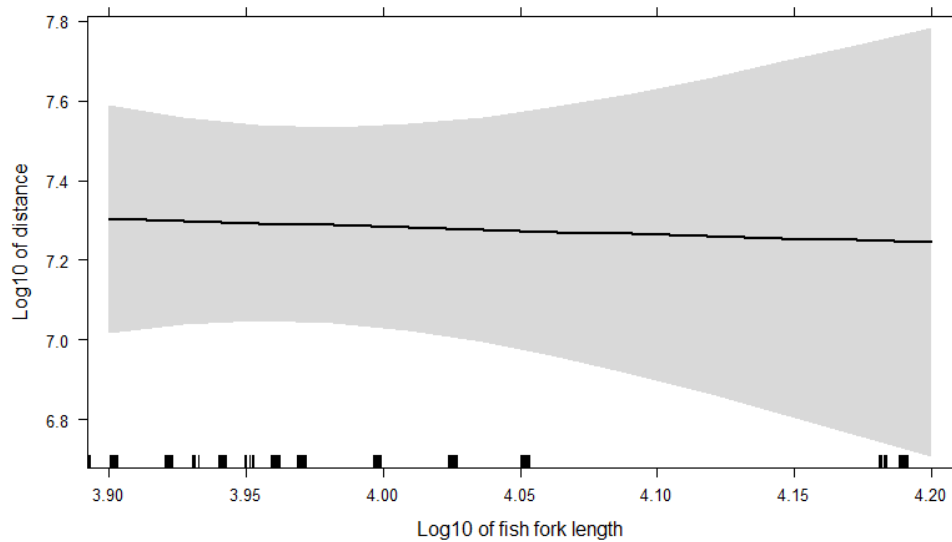


Fig. 4.7 General linear model of \log_{10} fish fork length against \log_{10} of distance covered found no significant difference in distance travelled based on fish size (grey area = 95% confidence interval)

Rate of movement analysis found that larger sea bass had a significantly higher mean ROM than smaller specimens (Pearson correlation: $r(31) = 0.44$, $p < 0.05$) (Fig. 4.8). The average ROM of tagged sea bass ranged from 0.01m/s^{-1} to 0.33m/s^{-1} .

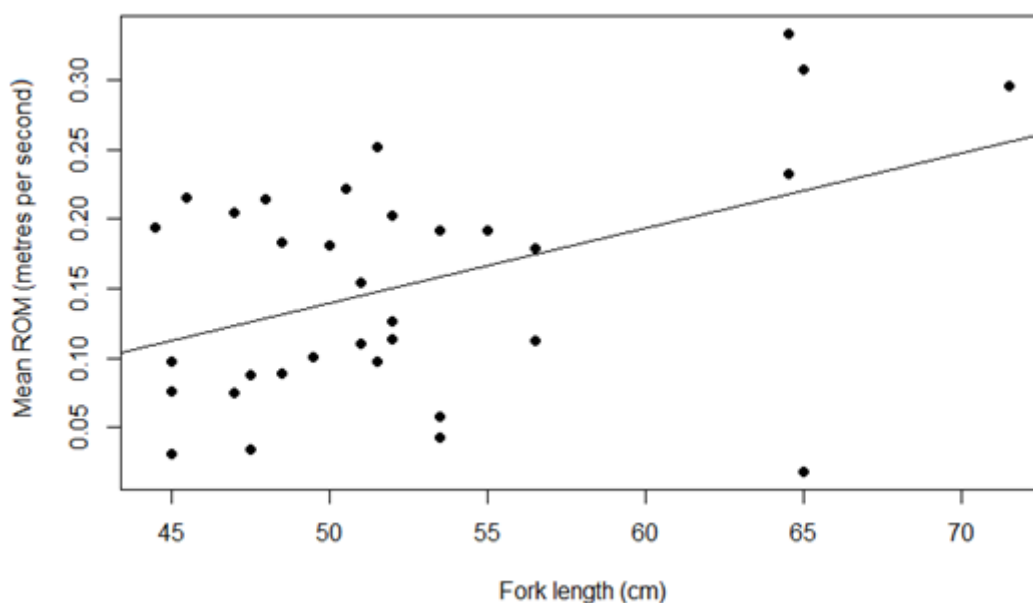


Fig. 4.8 Fish fork length (cm) against mean ROM (m/s^{-1}) found that larger sea bass had significantly ($p < 0.05$) higher swimming speeds than smaller specimens

Variation in swimming distances

The mean number of receivers a tagged sea bass was detected on was 2.3 (SD = 0.93) over the 12 month period from 01/07/2015 to 30/06/2016. The most receivers a single sea bass was detected on was five with fish 26225 released from receiver location 7 being recorded on receivers at locations 1, 2a, 6, 7a and 7b. During the 12 month period, a number of variations in swimming distances were identified from tagged sea bass. These behaviours were separated into four movement categories: (i) short distance repeat journeys (0-5km from release location), (ii) medium distance repeat journeys (5.1-20km from release location), (iii) medium-long distance journeys (20.1-50km from release location) and (iv) long distance journeys (>50km from release location).

Of the 38 fish detected 48 hours post release, 68.5% ($n=26$) were detected on a receiver a short distance (0-5km) from the release site only, though sea bass were not detected during variable periods of absence. Medium ranged movements were observed in 10.5% ($n = 4$) of tagged fish. Additionally, medium/long movements were recorded in 10.5% ($n = 4$) of fish

while an additional four tagged specimens (10.5%) were found to have undertaken long range movements.

Short range movements were recorded predominately for sea bass released/present in estuarine locations where dual receivers were deployed (receiver locations 2, 5, 7 and 8). These short range journeys represented 98.8% of the total number of journeys (1954 of 1977) recorded during this study. All short range journeys were recorded by sea bass released at estuarine locations. Medium range journeys were undertaken by sea bass from estuarine habitats to surrounding areas, often returning to their original release location. For example, fish 26228 travelled westwards from location 5 along the coastline to location 4 and back again, a journey which was undertaken twice (Fig. 4.9). These return journeys from location 4 to location 5 occurred on 29/10/15 returning on the 12/12/2015 (34 days) and from 26/02/2016 to 06/04/2016 (40 days).

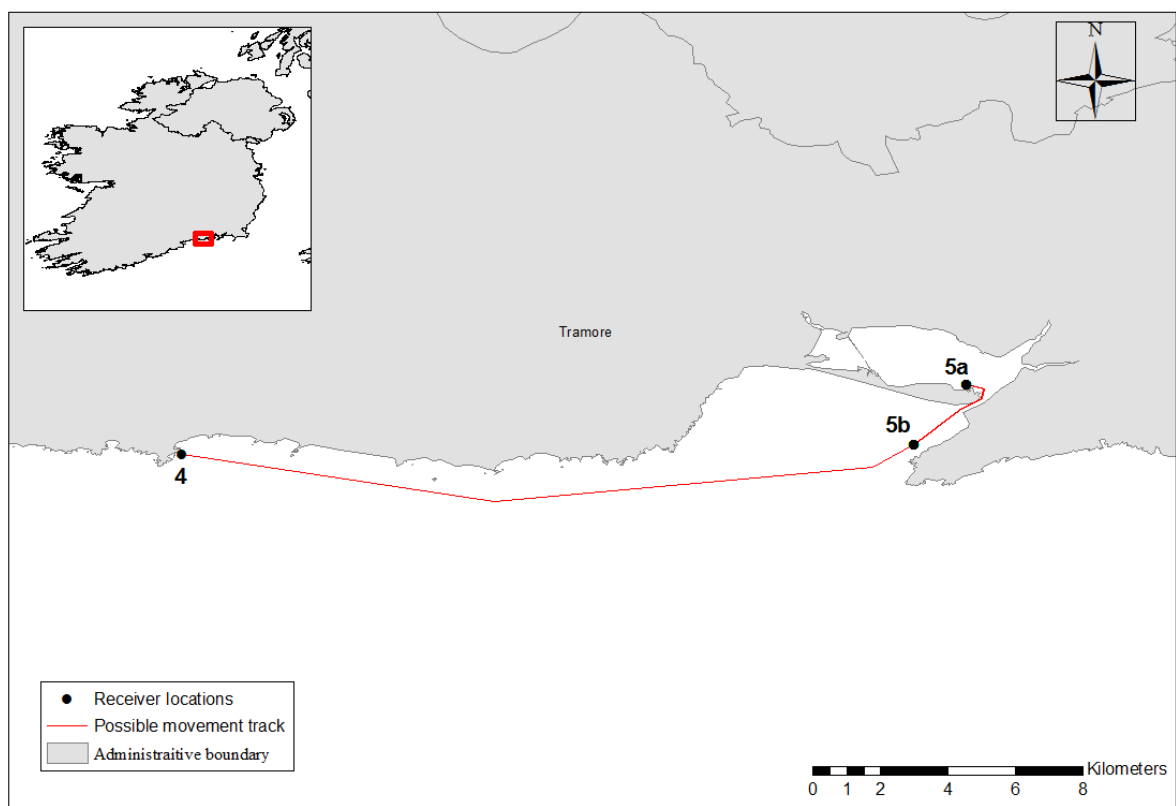


Fig. 4.9 Estimated medium range journey observed in fish 26228 which left receiver 5a, passing 5b and then on to location 4 before returning to location 5 again

An example of a medium/long range journey was observed in fish 26221 (Fig. 4.10) which left its release location at receiver location 3 after a short period of remaining within the locality (four days) before moving eastwards along the coastline to location 5, a journey which took five days during which the sea bass was also detected at receiver location 4. The journey from receiver 4 to the receiver 5a took 11.75 hours at a mean assumed swimming rate of 0.30 m/s^{-1} (or $0.53 \text{ body lengths per second [BL/s}^{-1}\text{]})$. The sea bass then left location 5, travelling westwards to location 4 after which it returned to location 5 again. After 20 days in location 5, the sea bass once again headed westwards, this time travelling as far as location 2 where it remained for 21 days, before returning to its original release position at location 3.

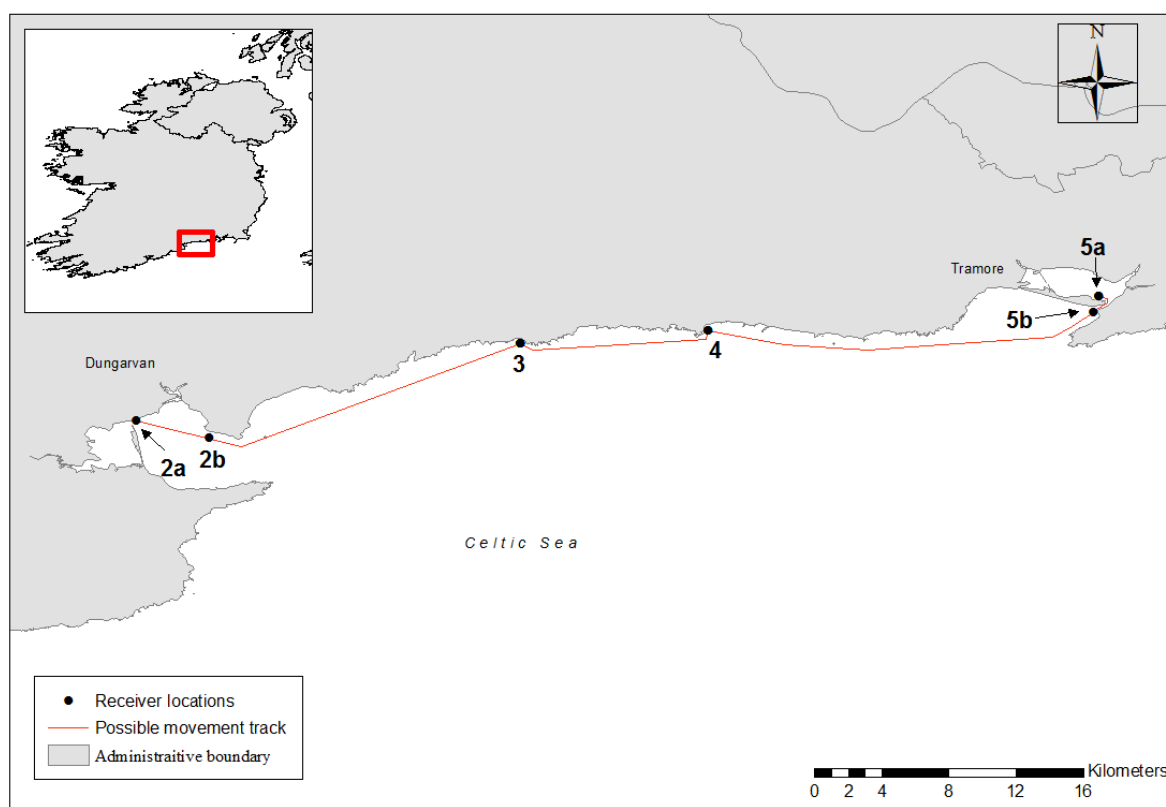


Fig. 4.10 An example of medium/long (20.1-50km) distance movement (journey timing: 02/05/2016 to 19/05/2016)

Of the four sea bass which recorded long range (>50km) journeys, three came from estuarine release locations (two from location 8, one from location 7) and one from a rocky shore release location (location 3). The average length of a long distance (>50km) journey was

63.8km (SD = 41.1). The long-range movement of fish 26215 (Fig. 4.11) estimated that the fish had travelled a distance of approximately 55.8km in 9.23 days, at a mean rate of 0.06 m/s^{-1} (0.1 BL/s^{-1}). This sea bass left location 8, having been present there for a period of 23 days post-release, and at the end of the study (30/06/2016), was present in the lower reach of the estuary above the 10a receiver.

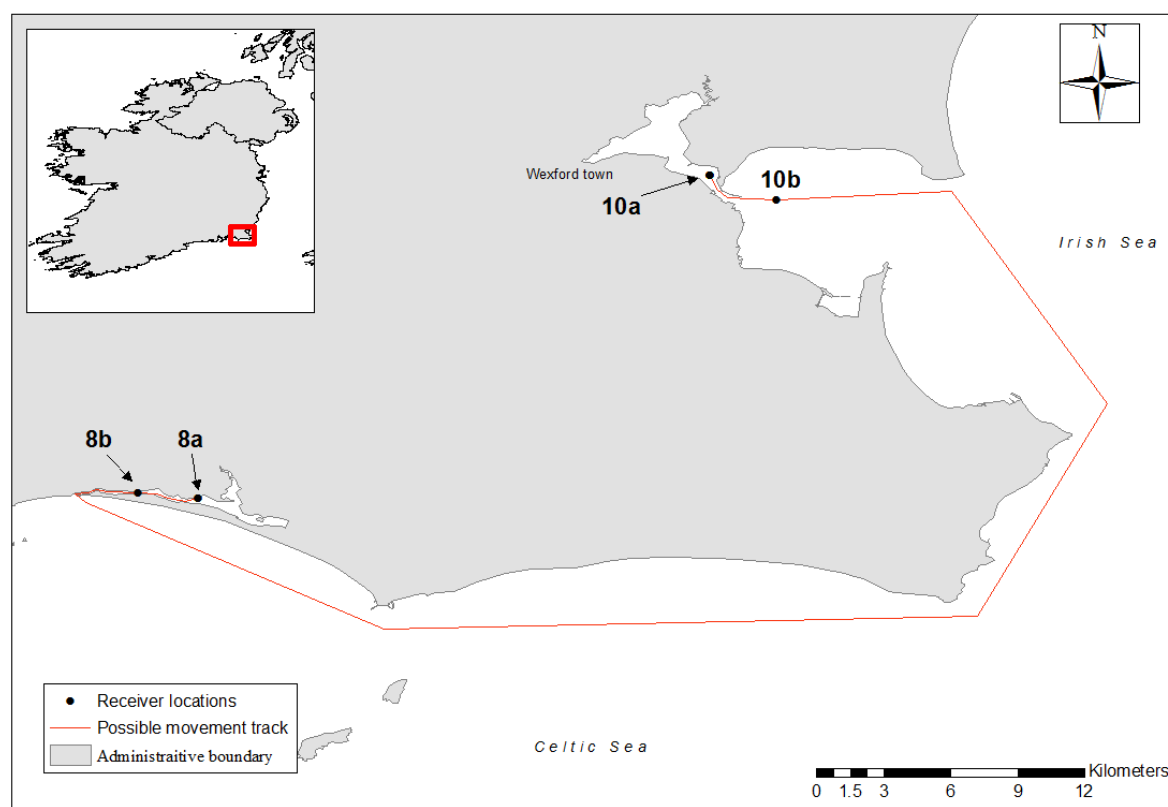


Fig. 4.11 Potential long distance (>50km) movement track of fish 26215 (journey timing: 16/05/2016 to 25/05/2016)

Evidence of extended periods of absence was also recorded in some sea bass. For example, fish 26225 (Fig. 4.12) was present for 15 days post-release in location 7 (its original release site), prior to travelling westwards and being detected on receiver 2a. This 95km movement took 3.5 days at a mean swimming speed of 0.31 m/s^{-1} (0.62 BL/s^{-1}). After a period of two days, this fish then proceeded to travel further westwards, reaching location 1 approximately 6.75 days later at a mean speed of 0.07 m/s^{-1} (0.13 BL/s^{-1}). This fish was detected at location

1 on seven separate occasions over the course of 56 days before leaving the area. The next detection of the fish was at location 6 after 240 days of liberty.

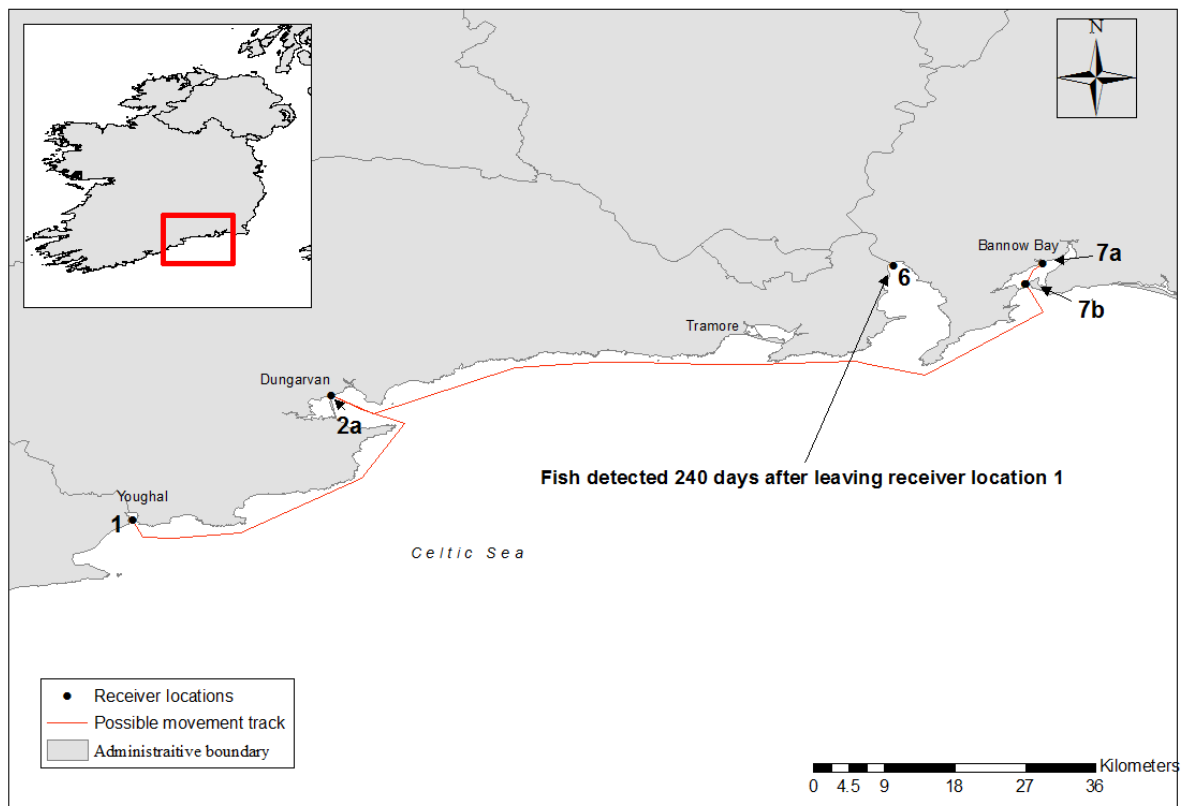


Fig. 4.12 Potential long distance (>50km) movements of fish 26225 (journey timing: 06/07/2015 to 07/06/2016)

Additionally, post-release, a tagged specimen released at location 8 on 20/11/14 was not detected by the receivers in the locality. This sea bass remained absent for over 284 days, after which it was detected at receiver location 1 over 110km away.

Discussion

Previous tag recapture studies have provided limited information regarding the inshore feeding/nursery area movements of sea bass, particularly along the southern coastline. A mark /recapture program, undertaken by Kennedy & Fitzmaurice (1972) found sea bass movements on southern coastlines to be essentially local, with recaptures coming from a

maximum distance of 67.6km away from release sites. This study provides a detailed indication and description of strong inshore feeding site fidelity within sea bass from inshore Irish waters and also shows that a proportion of the sea bass population remains inshore during the spawning season, suggesting the possibility of inshore spawning behaviour. Our study also found that sea bass activity and location use can differ significantly temporally, and by locality, and is influenced by light and tidal cycles. Finally, it was found that while the majority of sea bass movements occur over short distances, individual sea bass are capable of longer distance migrations while others show evidence of repeat journeys over medium distances (up to 20km), suggesting the possibility of habitual patrol routes use by individual fish.

Site fidelity and presence/absence periods

The sea bass deemed to be resident were all caught and tagged in estuarine waters suggesting that, for the duration of the study period, fish were more inclined to remain in estuarine locations rather than in exposed rocky habitats. Kennedy & Fitzmaurice (1968; 1972) suggested that sea bass in Irish waters spawn close to estuaries, noting the presence of ripe sea bass in the Blackwater estuary in the spawning period between February and June. It is therefore possible that spawning could occur in these locations once sexual maturity is reached (Kennedy & Fitzmaurice, 1972). Based on the periods of consecutive absence for resident fish (maximum of 10 days), it is highly unlikely that they would have undertaken significant migrations during the spawning period. Were inshore spawning potentially to occur, it could therefore be assumed that it could result in the delivery of larvae into suitable nursery habitats, far more rapidly than spawning from offshore locations, as suggested by Kennedy & Fitzmaurice (1968; 1972) or that the area for spawning extends outwards from inshore to offshore waters. Retention of larvae within these estuarine locations may be

possible through tidal stream transport to nursery areas further up estuaries, like larvae of the Japanese sea bass *Lateolabrax japonicus* (Secor, 2015), and with larvae also being retained in backwater eddies. These findings are in contrast to those of Claridge & Potter (1983) and reported in Carroll (2014), who suggested that sea bass spawning events in British waters could only occur in fully marine environments away from estuaries.

It may also suggest that the residency behaviour exhibited by these 11 fish may be as a result of poor conditioning and, as a consequence, a failure to mature in that year, which would therefore result in the sea bass not initiating migration to offshore spawning location. This could also be interpreted as potential evidence of skipped spawning, which has previously been recorded in striped bass, *Morone saxatilis* (Raney, 1952; Secor & Piccoli, 2007). Life-history theory suggests that fish may skip reproductive events after initial maturation to maximize lifetime fitness with studies on Atlantic cod (*Gadus morhua*) findings that up to approximately 30% of the spawning stock, similar to the percentage of resident inshore sea bass recorded in this study, may skip spawning annually (Jørgensen *et al.*, 2006; Skjæraasen *et al.*, 2012). The presence of at least one tagged sea bass each month post-release at the estuarine locations 2, 5 and 8 (though none of the three tagged sea bass from location 2 were recorded during September just after their release) suggests that inshore areas can support sea bass during colder seasons. However, the colder waters experienced by sea bass in these inshore locations could limit gonad maturation, as has been documented in adolescent sea bass (Pickett & Pawson, 1996; Pawson *et al.*, 2000), over the winter and early spring months, thereby increasing the likelihood of skipped spawning in adult specimens.

The 71.1% (n = 23) of tagged sea bass deemed to be non-resident, were however present at various times over the period of full acoustic deployment. Their reduced presence in areas covered by acoustic receivers, suggests a higher level of movement between areas, potentially both inshore and offshore. These findings are similar to those reported by Doyle *et al.* (2017) who recorded an almost complete absence of acoustically tagged sea bass in the

Cork Harbour region during winter and early spring periods in 2014 and 2015, though these results may be linked to unfavourable environmental conditions within the locality, as have been previously highlighted by Kennedy & Fitzmaurice (1972). It is highly possible that a proportion of these non-resident sea bass in this study may have migrated offshore to spawn. It was found that 21 of the 23 non-resident sea bass were absent for 20 days or more consecutively during the assumed spawning period. Based on the upper average ROM recorded in this study (0.33m/s^{-1}), this could potentially result in a return straight-line migration of 285km from origin. This behaviour would be in accordance with the evidence presented in Chapter 5 which recorded offshore migrations of adult sea bass from the southern Irish coast during the peak spawning period between April and June 2016.

Changes in the abundance and distribution of prey species during early spring may have resulted in sea bass being absent from the rocky shore habitats, favouring feeding in more productive estuarine zones. However, the distribution of receivers along the coastline must be taken into account, with areas of rocky habitats having less coverage than relatively bottlenecked estuarine zones. It may be possible that sea bass frequent these more exposed locations during this period but investigation of this will require further research.

The close proximity of location 7 and location 8 highlighted the low RI results of sea bass from some locations when compared to others. The low RI value for location 7 (0.08) in addition to the absence of tagged specimens, particularly those originating at location 7, from December to the start of May, could be due to unfavourable environmental conditions with the estuary receiving more freshwater input than other locations. It may also be possible that the fish at location 7 display more varied site fidelity throughout the year than those at location 8, with sea bass leaving the estuary during winter and spring and remaining in the locality (but outside receiver range) and returning in summer.

The movement of sea bass between receiver locations also revealed interesting results concerning location 8. While specimens released from location 8 were detected at 3 other areas, no migrants from any other release sites were recorded at location 8. The relatively narrow entrance of location 8 (approximately 90 metres) when compared with other larger estuaries at location 2, 5 and 7 (approximately 400, 200 and 260 metres respectively) may have resulted in sea bass bypassing it or migrating past the island to the south of it, approximately 1.5km from the shore. It was also noted that, while tagged sea bass from more eastern sites (location 7 and 8) were detected on receivers further west, no tagged specimens released from location 2, 3 or 5 in the west of the study area were recorded to have moved east beyond location 6. It may be possible that tagged sea bass from these locations do migrate east along the coast but do not enter estuaries as they travel.

Light, tide and temporal changes in detections

This study represents the first reported observations of sea bass behaviour with respect to tide and light cycles in the wild. For all tagged sea bass detected over the February to June period peak detection rates were at dawn and dusk, showing that sea bass activity is highest during these periods. It may therefore be possible the foraging in sea bass is predominately crepuscular, with dawn and dusk periods having the optimal light level for sea bass movement and foraging, when light levels are low enough to offer some protection from predators, such as seals, but bright enough to spot and target prey. The absence of significant differences in detection rates found between diurnal periods, concerning resident fish only could possibly be attributed to more uniform movement patterns over a 24 hour period. Pickett & Pawson (1994) also suggested that the absence of sea bass from inshore locations during day periods may be due to disturbance from human activities and this may contribute to the lower rate of detection. Low detection rates during the night period may be due to sea

bass resting in areas out of the receiver line of sight, such as in hollows or behind small reefs, or leaving the area of the acoustic array completely. Findings from Australasian snapper (*Pagrus auratus*) and striped bass (*Morone saxatilis*) acoustic tracking in estuaries have suggested that the lower detection rates recorded in this study in acoustically tagged sea bass at night may be due fish moving into shallower waters under the cover of darkness and therefore potentially out of the receiver detection range (Harthill *et al.*, 2003; Ng *et al.*, 2007 respectively). Additionally, How & de Lestang (2012) found that increasing ambient noise during night may have a significant effect on the detection ability of the receivers thus reducing their efficiency. Despite these caveats, it is reasonable to conclude that reduced luminosity levels during the dawn and dusk periods are most likely associated with increased activity and foraging. Evidence of such behaviour has been previously recorded in predatory fish, such as the European eel (*Anguilla anguilla*), in lacustrine environments (Barry *et al.*, 2015).

Tidal influence on detection rates revealed some interesting patterns. Receivers 2b and 5b, located towards the mouth of main channel within their respective localities, were both found to have significantly higher detection rate on ebbing tides. This may suggest that sea bass within these localities leave the inner areas of the respective bays earlier on the ebbing tide, holding position in eddies or hollows on the seabed, at the mouth of the main channel. Sea bass have been documented under laboratory conditions to maintain position in water flowing at a rate of 80cm/s^{-1} (Pickett & Pawson, 1994). This strategy allows feeding sea bass to predate on prey items often concentrated in estuarine areas due to tidal currents and has been recorded in adolescent and adult sea bass (Kennedy & Fitzmaurice, 1972; Pickett & Pawson, 1994). Evidence of this behaviour can be observed in detections rates at different times of the tidal cycle in location 5, with sea bass potentially feeding at the mouth of the estuary on the ebbing tide and moving into the estuary to feed on the flooding tide. The opportunistic usage of tidal flow for feeding and movement at location 5 shows evidence of optimisation of

foraging and movement behaviours by sea bass. The absence of a significant difference in detection rates recorded in resident fish on the upper and lower receivers at location 8 with respect to tidal flow may be due to the more uniform habitat (a more defined main channel) at the location or it may also be possible that fish at location 8 migrate more in synchronicity with tidal flows. However, a similar pattern to what was found at location 5 for all tagged specimens, was observed in resident tagged sea bass at location 8, with a significantly higher detection rate on the lower receiver (8b) on the ebbing tide and on the upper receiver (8a) on the flooding tide. There is no explanation as to why this pattern was not present in all tagged sea bass (both resident and non-resident fish combined) at this location.

The decrease in detection rates throughout the course of the study period, indicating that tagged specimens were using the areas around the receivers less as the study continued, contrasts with the increase in the numbers of individual tagged specimens present throughout the period of full acoustic receiver deployment. While it appears that adult sea bass return in number to inshore locations during late spring and early summer (Kennedy & Fitzmaurice, 1972; Pawson & Pickett, 1996; Pawson *et al.*, 2007; Doyle *et al.*, 2017), they also may use these locations less, passing through quickly or foraging in other areas. The higher detection rates observed earlier in the season at some receivers (5a, 8a and 8b) may be as a result of lethargy in tagged sea bass due to colder water temperatures (Kelley, 1979) and, therefore, spending more time in the vicinity of the receiver. The decreasing detection rate may be as a result of a change in prey species distribution with tagged specimens having to forage further afield as the study period continued (Kelley, 1979). Previous research regarding the effects of the surgical insertion of the acoustic tag into fish have observed have negligible effects on the swimming ability, buoyancy, orientation and feeding ability (Bridger & Booth, 2003).

Movements and distance covered

Although the results of the mixed model were not significant, smaller sea bass tagged in this study tended to travel more frequently than larger fish. In contrast, Pawson *et al.* (1987 (b)) and Holden & Williams (1974) found that larger sea bass were more mobile and covered larger distances in studies conducted in British waters. While this phenomenon has already been documented by Pawson *et al.* (2007), this result may be explained by predation ability differences in sea bass depending on their size. Larger sea bass have big mouths with the characteristic “Gladstone bag shape” (buccal cavity) which is evident in fish in the order Perciform (Pickett & Pawson, 1994). This enables them to eat larger and more varied prey species, thus reducing the need for excessive movement. Larger sea bass also tend to be more piscivorous, consuming larger, more nutritious prey, often predating on flatfish or other fish species, which reduces their need to feed as frequently. Smaller sea bass have a less varied diet, often feeding on smaller, less nutritious prey therefore resulting in increased movement while foraging to satiate their appetite (Kelley, 1987). In teleost fish such as sea bass, larger specimens possess more dark muscle along their flanks enabling them to swim at higher average speed for longer than small fish (Pitcher & Hart, 1982) which would account for the significantly greater ROM observed in larger sized sea bass. The upper range of mean ROM observed in this study is also in accordance with findings from Sibert & Nielsen (2013) estimating ROM for a 1.5kg sea bass at 0.19m/s^{-1} to 0.31m/s^{-1} .

Some 98.8% of all journeys ($n = 1954$) recorded in the 12 month period from July 2015 to June 2016 were short range journeys (0-5km), all of which were undertaken within estuarine locations. As 68.5% of all tagged sea bass were only detected less than 0-5km from their release site over this period, it might be speculated that residency in relatively discrete inshore locations is the predominant behaviour of the species in Irish waters for the majority of the year. These findings are in accordance with those reported by Doyle *et al.* (2017) who found that sea bass which were resident in Cork Harbour had a home movement range of 0-

3km. However, receivers in this study also recorded longer range movements from tagged specimens. The possible causes of repeated medium range (5.1-20km) journeys observed in this study, such as recorded by fish 26228, are unknown. The presence of other tagged sea bass for the duration of these journeys at the site of journey origin suggested that poor environmental conditions were not the cause of these migrations.

Previous studies have shown that sea bass can travel long distances over relatively short periods of time with a specimen reported to have travelled up to 1200km in less than two months (Pawson *et al.*, 2008). Another tagged sea bass travelled three weeks post-release from an inshore location on the Irish south-west coastline to be caught 60km off the south east coastline of Ireland (Pawson & Pickett, 1987). The movement speeds and distances covered by tagged sea bass in this study were variable. Fish 26215 in this study travelled east over minimum movement distance of approximately 55.8km at a mean rate of 0.1 BL/s^{-1} , though it may be possible that the actual journey distance could have been considerably longer, particularly if the fish went to the south of the Saltee Islands located to the south of Kilmore Quay, Co. Wexford. In contrast, fish 26225, showed a much higher mean swimming speed of 0.62 BL/s^{-1} as it travelled west along the coast possibly indicating a certain proportion of inshore sea bass form an offshore component, or indeed, interact with a separate offshore fish, a conclusion which was also reached by Holden & Williams (1974).

Recommendations

Based on the results of this study and the experience gained through experimental design, it is suggested that in order to gain more accurate insights into sea bass behaviour, particularly concerning small scale movements (home ranges) and behaviours, future acoustic studies could concentrate on one study location with blanket receiver coverage. Habitats which may provide a suitable study area for such an investigation include areas of structure such as reefs

or within estuaries. Additionally, lines of receivers extending out seawards from the coast may provide a better insight into sea bass behaviour in deeper waters, further from the shore. Although the science of mixed modelling is very dynamic and subject to change, the statistical methods which have been adopted in this study are in keeping with current best practice and have been used in other previous acoustic studies (Zuur *et al.*, 2009; Harasti *et al.*, 2013).

The absence of an offshore fishery for sea bass within Irish waters may also be contributing to the perception that there is more localisation of stocks in Ireland than may be the case (Pawson & Pickett, 1987). This is supported with evidence from research surveys and commercial discard monitoring documenting the existence of sea bass in Irish offshore locations (see Chapter 2). The results of this study will add new insights to inform best management practices for conservation and protection.

Acknowledgements

The authors would like to thank the following people for their assistance during the undertaking of this research: University College Cork, The Beaufort Marine Research Award, The Marine Institute (Nigel Bond, Alan Drum, Joe Cooney, Dermot Fee and Robb Bunn), Dr Thomas Reid (University College Cork), Jim Hendrick (ProbassFisher, Co. Wexford), Sean Jordan (Bass Fishing Wexford, Co. Wexford), Cian O'Halloran (Absolute Fishing, Co. Waterford), Dr James Barry and Dr Sean Rooney (Inland Fisheries Ireland), Kilmore Harbour Office, Waterford Co. Council and the Commission for Irish Lights.

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Chapter 5

**Identification of potential spawning locations of the sea bass
Dicentrarchus labrax through the use of pop-off satellite tags
(PSATs) in the Celtic Sea**

Abstract

A total of 12 adult sea bass were tagged with pop-off satellite archival tags (PSATs) in Irish coastal waters and in offshore waters in the north-east Celtic Sea between 2015 and 2016. This study represents the first reported use of such tags on European sea bass. Fish movement data were successfully recovered from five of the 12 tags deployed, three from fish released in inshore Irish waters and two from fish released offshore in the eastern Celtic Sea. Interpolated tracks show that fish tagged on the southern Irish coast migrated in a south-easterly direction to the eastern Celtic Sea in a period which is assumed to coincide with spawning. Tracking data also suggested that sea bass tagged in offshore locations were present within the same area. A sea bass tagged at an inshore location on Ireland's south coast travelled north and was present on the north-west coast of England during the peak spawning period. All three fish tagged inshore were found to exhibit inshore site fidelity, returning to the same general location (within 50km) of their original release site. The findings of this study suggest that at least some sea bass that originate in both Irish and British coastal waters aggregate in the eastern Celtic Sea during the assumed spawning period prior to returning to inshore waters and that the use of PSATs as a method of tracking sea bass movements is possible. It is also suggested that the management of sea bass in the Celtic Sea must take into account the ability of the fish to migrate considerable distances, across different jurisdictions and management areas.

Introduction

Within the open marine environment, fish movements can be tracked through the use of pop-off satellite archival transmitter (PSAT) tags. These tags, typically mounted to the dorsal flanks of the fish, archive various environmental parameters dependant on tag manufacturer and tag type (Walli *et al.*, 2009). Though traditionally fitted to larger species such as bluefin

tuna, *Thunnus thynnus*, (Abascal *et al.*, 2016), sailfish, *Istiophorus platypterus*, (Hoolihan & Luo, 2007) and swordfish, *Xiphias gladius*, (Abascal *et al.*, 2015), advancements in tag technology have resulted in streamlined, lightweight tags which can be used on smaller fish species. Unlike traditional archival tags, PSAT tags are programmed to detach at a pre-defined date and time, transmitting archived data via the ARGOS satellite network (Coyne & Godley, 2005) resulting in a method of biotelemetry that is particularly useful in fisheries where chances of tag recovery are low. The data provided by archival tagging plays a crucial role in the understanding of fish migrations, particularly concerning the identification of potential spawning locations (Nielsen & Sibert, 2007).

Extensive tag/recapture studies using standard identification tags on European sea bass, *Dicentrarchus labrax*, in British waters have been previously undertaken by Holden & Williams, 1974; Kelley, 1979; Pawson *et al.*, 1987; Pawson *et al.*, 2007; Fritsch *et al.*, 2007 and Pawson *et al.*, 2008. In late spring and summer seasons, adult sea bass can be found in relatively discrete inshore regions which they may frequent annually (Pawson *et al.*, 2008). During late autumn and early winter, sexually mature sea bass begin migration to spawning locations believed to be predominately located in deep, warm offshore waters (Thompson & Harrop, 1987). Spawning location is believed to be highly influenced by water temperature, with minimum threshold of 8.5°C to 9.0°C required to allow for larval survival and development (Thompson & Harrop, 1987; Pickett & Pawson, 1994). As a result, tag/recapture studies have found that sea bass on western British coasts move south into the Bristol Channel and English Channel, while those tagged in the southern North Sea also move south into the waters of the English Channel. Sea bass in the English Channel have been found to move offshore to form spawning aggregations (Thompson & Harrop, 1987). The distance that sea bass may travel can be considerable, with previous studies having recorded movements of between 750km (Kelley, 1979) to 1200km (Pawson *et al.*, 2007).

In contrast to the research carried out in British waters, little is known about the spawning migrations of sea bass found in Irish coastal waters. Kennedy & Fitzmaurice (1968; 1972) found the presence of sea bass eggs at five separate locations on the south coast and suggested that spawning events occurred in inshore waters, often close to large river estuaries. To date, however, sea bass larvae have not been reported in inshore Irish waters. Results from tagging of sea bass during the 1970s with identification tags along the south Irish coast showed a highly localised distribution of the species with the furthest distance travelled recorded at 67.2km, with all recaptures being made in inshore waters (Kennedy & Fitzmaurice, 1972). However, recent acoustic telemetry research on sea bass in Irish waters has suggested the possibility of annual migration to offshore waters, coinciding with assumed spawning periods (see Chapter 4; Doyle *et al.*, 2017). Additionally, a study by Pawson *et al.* (2007) recorded a recaptured sea bass released from inshore waters on the western Welsh coast in inshore waters along the south-western Irish coastline, highlighting evidence of movement between sea bass of both Irish and British origins. In addition, a sea bass tagged in inshore waters in south-east Ireland in 2016, was re-caught 203 days later over 350km away in Morecambe Bay on the north-west coast of England (Marine Institute, unpublished) further suggesting that Irish sea bass may undertake long range migrations across open waters.

The objective of this study was to track adult sea bass released from Irish coastal waters and offshore in the north-east Celtic Sea using PSATs in order to identify the locations where they may spawn. The extent of post-migration feeding site fidelity of sea bass tagged in Irish inshore waters was also investigated.

Materials and methods

Specimen acquisition

The specimens of sea bass tagged in this study were obtained during systematic and extensive sampling program over two years on the southeast coast of Ireland to carry out conventional, acoustic and satellite tagging and tracking and biological analyses of sea bass aimed at understanding the behaviour and migration of sea bass from Irish waters and the Celtic Sea. The selection of specimens to being fitted with PSATs was based on fish length, with fish over 42cm selected as they were deemed to be adults (Inland Fisheries Ireland, 2014) and therefore more physically adept at carrying an externally mounted tag. Efforts were made to use larger specimens (over 3.62kg) where possible.

Acquisition of specimens was carried in accordance with a derogation obtained from the Sea Fisheries Protection Authority (DSR 02/2015). Based on extensive local angling and commercial fishing knowledge prior to 1990, sampling was conducted in areas where the chances of encountering large adult sea bass were likely to be high. Seine netting (net specifications: 100m long x 4m deep; wings = 42m wings of 210/30 x 80mm stretched mesh knotted nylon; cod-end = 16m of 210/12 x 20mm stretched mesh knotless nylon) was undertaken in the Cullenstown, Co. Wexford in April, 2016, with eight fish tagged over three days. Inshore trawling took place on board the *MFV Boy River* in the Waterford estuary using a small otter trawl with a headline height of 3 meters in February of 2016, with one fish tagged at this location. Tows varied between 10 and 20 minutes in duration.

Targeted offshore sampling was undertaken on the *MRV Celtic Voyager* during March 2016. A pelagic trawl with a headline height of 7m was used to target sea bass in areas where catches of sea bass had been previously identified based. The net was towed approximately 3-5m off the seafloor at a speed between 3.5 to 4.5 knots. Tows duration was between 20 and 40 minutes. This method resulted in the tagging of a single specimen. Two further sea bass

were tagged and released in the eastern Celtic Sea during the annual Irish GroundFish Survey (IGFS) in November 2015 on board the *MRV Celtic Explorer*. IGFS stations were fished during daylight hours to ensure standardisation of results. At each survey station a 30 minute trawl along the sea floor was conducted. The sampling gear used on the IGFS was the French Grand Overture Verticale (GOV) net, designed to target species feeding on and above the seabed. The trawl headline height was 4.5m and speed was maintained at approximately four knots for the duration of the tow. The net spread was achieved through the use of Morgere FP 10 trawl doors mounted on either side of the net. Sensors were fitted to the net and trawl equipment to ensure that the net fished correctly (Marine Institute, 2012).

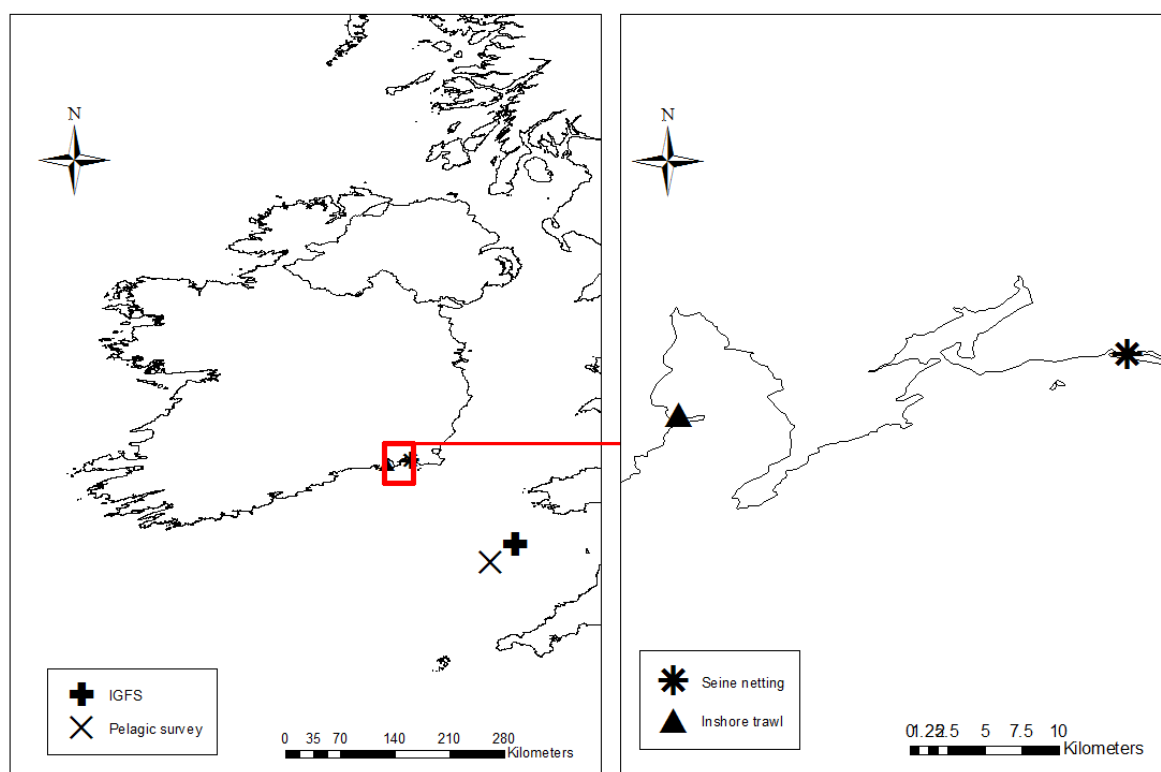


Fig. 5.1 Offshore specimens were tagged and released in the eastern Celtic Sea while inshore specimens were tagged in two separate estuary locations, located only 17km apart

PSAT tagging procedure

Tagged specimens were first assessed for symptoms such as reduced gill activity, excessive bleeding and barotrauma prior to ensuring suitability for tagging. The sea bass were placed in a holding tank/keep net to recover post-capture before being placed into a 2-phenoxyethanol and seawater mixture (approximately 40ml in 80 litres of seawater) to induce anaesthesia. Once the specimen had lost equilibrium and gill rhythm was slow but constant, the specimen was measured for fork length (cm) and weight (grams) before being placed in a trough lined with a sterile surgical drape. A cloth was placed over the specimens' head to reduce stress and a constant supply of seawater-anaesthetic mixture was passed over its gills.

The mounting of the tag bridal was similar to the method described in Økland *et al.* (2013). The PSAT tag bridal was composed of two strips of hardened plastic (40mm x 10mm) with rubber backing plates, to prevent injury and irritation to the sea bass, connected via a braided section of marine-grade nylon. Medicated iodine solution was used to sterilise the area of needle insertion on the dorsal flanks. Mounting of the bridal was achieved by the passing of two spinal cannulae needles (18G x 3.5 inch; BDTM, USA) through the dorsal musculature of the sea bass between the primary (spiny) and secondary (soft) dorsal fin. The exact site of needle insertion was identified by holding the backing plates in position and lining them up on either side of the dorsal flanks. Once the needles were inserted, the cannulae inserts were removed and a 'U-shaped' section of autoclaved 0.9mm stainless steel wire was inserted into the needle hollows. The needles were then slowly withdrawn, leaving the wire in place and allowing for the tying off of the stainless wire by hand, with care taken not to overtighten. This method of tagging allowed for lateral movement of the tag while also reducing and evenly distributing drag on the sea bass. The PSAT tag was then attached via a stainless steel clip to a heavy gauge braided nylon section (three to four inches long), externally attaching both plastic plates to allow for lateral movement of the tag on the bridal. Additional red and yellow Floy tags carrying an identification code in the form of "IRLXXXX" were inserted

into the dorsal of each fish to the area approximately 3-5cms in front of the PSAT bridle. Tagged specimens were then allowed to recover in a tank of aerated seawater for up to 60 minutes prior to being released, once equilibrium and rhythmic gill movement had returned. Data for tagged sea bass is displayed in Table 5.1.

Tagging procedures undertaken in this study were carried out under licence by the Health Products Regulatory Authority (Licence No.: AE19121/P001) and with approval from the University College Cork's Ethics Committee.

Table 5.1 PSAT tagged fish information and tag deployment dates

PSAT ID	Capture method	Deployment date	Weight (g)	Fork length (cm)
148148	IGFS 2015	26/11/2015	3351	62.5
145137	IGFS 2015	26/11/2015	2696	56.5
145143	Inshore trawl	16/02/2016	2600	57
145142	Pelagic survey	17/03/2016	1295	46
145152	Seine netting	19/04/2016	3550	64
145141	Seine netting	19/04/2016	2360	52
145135	Seine netting	19/04/2016	2360	54
145144	Seine netting	19/04/2016	1960	53.5
145151	Seine netting	21/04/2016	2890	61
145149	Seine netting	21/04/2016	3730	66
145145	Seine netting	21/04/2016	3770	64
145146	Seine netting	20/04/2016	1920	51

Tag specifications

Release dates and times for SeaTag-GEO PSAT detachment were user defined with offshore tagged sea bass specified to detach during the assumed peak spawning season (April to June) and inshore tagged sea bass scheduled to detach in August/September, to identify potential inshore feeding and nursery site fidelity post-spawning migration. Detachment of the tag from the fish at the designated time is achieved via the detonation of a small charge of “Quikburst” powder, supplied by the tag manufacturer, in the nose-cone burn chamber of the tag.

The SeaTag-GEO was programmed to release from the fish if the temperature or light levels were below manufacturers pre-set thresholds for an extended period of time, which may have indicated a dead or dying fish in cold, dark waters. Once detached, the archived data were transmitted from the tag via the ARGOS satellite network. Data were transmitted in packets and contained daily summaries of archived environmental data.

The data recorded by SeaTag-GEO tags included: the daylight length (± 2 seconds); time of local apparent noon (± 1 second); minimum and maximum daily water temperature ($\pm 0.002^{\circ}\text{C}$); maximum observed temperature rate ($\pm 0.001^{\circ}\text{C}/\text{minute}$) and readings from a 3-axis internal magnetometer with a 10nT reporting resolution which archived readings from the earth's magnetosphere. Ambient sea water temperature readings were recorded by an inbuilt thermometer, while the corresponding satellite observed sea surface temperatures were provided by Collecte Localisation Satellites (CLS) through the use of the ARGOS satellite network. To reduce the potential for biofouling on tag surfaces, tags were treated with a light coat of marine-grade varnish, as per the tag manufacturer's instructions.

The level of light intensity was calculated as the time of local apparent noon, the point halfway between light levels rising above the threshold of 1.4 Lux in the morning and decreasing below 1.4 Lux in the evening. The tag records daily light intensity (solar panel voltage) for use in estimating geolocation error estimates and for diagnostic purposes, with the reporting of low light and short day length values evidence of potentially unreliable longitudinal calculation and longer days having a higher degree of accuracy. Tag accuracy for the calculation of longitude was to within $\pm 0.5^{\circ}$, equating to a distance of approximately 30 nautical miles at the equator. Magnetic field intensity data was sampled every four minutes. Magnetic field values typically increase with increasing distance from the equator, but are disturbed in areas of magnetic anomalies such as areas of volcanic rocks. In addition, tags in the vicinity of large metallic structures may report erroneous values due to compromised magnetic field readings. The mean of the centre 80% of magnetic readings was

used to calculate the daily estimated latitude, along the line of longitude established by light observations (Desert Star Systems, 2016). The predicted mean accuracy of this method is to within approximately 39 nautical miles (72.2km)

Daily minimum and maximum water temperatures were recorded by the PSATs. A total of three sea surface temperature (SST) observations were used in aiding geolocation. Skin SST refers to satellite observed water temperatures in the upper millimetres of water at the sea surface. Foundation SST corresponds to the temperature at an indeterminate depth where diurnal variations no longer affect daily temperatures. Between these two layers is the sub-skin SST where modelled values based on wind minimising the temperature gradient between skin and foundation SST were calculated. Due to the assumed behaviour of the sea bass swimming below the skin and sub-skin layers, foundation SST was used in this study, typically corresponding with the average daily temperatures recorded on the PSAT. The average SST gradient varies longitudinally, between 45° North and 45° South by approximately 0.4°C/degrees Latitude while the differential between the skin SST and foundation SST is commonly around 2°C. Therefore, mismatches between tag reports and applied SST model can result in a 5 degree latitudinal error (Marco Flagg, pers.comm.). A bias compensation between PSAT recorded temperature and foundation SST was conducted based on the ARGOS detected location of tag detachment.

Initial track construction was undertaken using SeaTrack, a Desert Star System developed software, which estimated geolocation points using the intersection of light (longitude) and magnetic field (latitude) data. These tracks were refined by CLS which undertook “Track+Loc” processing on the transmitted data to produce more accurate estimated geolocations, with cross-validation between the two methods. The aim of track construction was to estimate a daily location for each fish based on a combination of magnetic field readings, light levels and water temperature data. This was achieved through the use of a space-state model which worked off the principle that the daily location is the unknown state

of a dynamic system governed by a dynamic ‘random walk’ model. Therefore, the sequence of the daily state follows a Markovian process (Stehfest *et al.*, 2014) whereby the probability of a fish being at a location at a certain time-step is determined by its estimated location at the previous time-step. This ‘hidden’ daily location is directly linked to the preceding day through the magnetic field, light intensity and water temperature data in addition to the assumed swimming behaviour of the fish (deemed to be non-daily surfacing).

The state space model used to calculate geolocation operates using a Grid Filter dividing the map into a resolution of 0.1 x 0.1 degrees grid cells. The Grid Filter (Nielsen *et al.*, 2014) is based on a recursive Bayesian estimation technique similar to Kalman filtering. The initial step of the model undertakes the solving of the advection/diffusion equation at each time-step to estimate the 2D probability of the animal’s presence within the grids. The archived environmental data stored on each tag were then used to calculate and updated position. The model assessed each of the environmental variables and then weighted them whereby the most reliable variable (the one with the least variance) was designated the greatest weight within the model. These combined steps were averaged over a 24 hour period to estimate the daily geolocation of the fish. Tracks were constructed between daily estimated geolocations in chronological order using opportunistic ARGOS transmitted locations (where the tagged fish may have come to the surface) and the coordinates of tag deployment and detachment as fixed anchor points. The confidence intervals (50% and 95%) for daily locations were produced based on the semi-minor and semi-major error covariance matrix of the daily distribution. Therefore, PSATs which transmitted a higher proportion of archived data resulted in a higher degree of accuracy regarding track estimation. A comprehensive description of method of track construction can be found in Biais *et al.* (2017).

Results

Tag success rate

A total of 12 PSAT tags were deployed with all fish swimming away strongly post-tagging. Data were obtained for five tagged sea bass (41.6%). Of the tags which reported data, three were from sea bass tagged in inshore Irish waters (145143, 145144 and 145152) and two were from specimens tagged offshore in the eastern Celtic Sea (145137 and 145142). Tags 145137 and 145148 were recovered from the western coast of Britain and returned, however, no data were recorded on tag 145148. Tag 145141 detached one day post-release and floated north to the southern coast of Scotland. All other tags failed to communicate with the ARGOS satellite network. The detachment dates, transmitted by ARGOS, showed that three tags detached later than the user-defined settings, while the remaining two detached prior to their scheduled time (range of -96 to +76 days; mean = 62.6; SD = 28) (Table II). Tag retention duration on specimens varied from 38 to 256 days (mean = 150.4, SD = 79.1). The percentage ratio of PSAT mass to fish body mass varied between 1.11% and 3.22% (SD = 0.58). There was no correlation between tag retention duration and specimen size (Pearson correlation, $p > 0.05$).

The number of messages received from each tag ranged between 35 and 1199 (mean = 295.8; SD = 452.3). Each message received contained a reading of the magnetic field strength, the time of noon, day duration (measured in seconds), observed water temperature and tag status information.

Table 5.2 Retention periods for successfully transmitting PSATs

PSAT ID	Pre-defined detachment date	ARGOS transmitted detach date	Difference (+/- days)	No. of days of tag retention	No. of messages received	Period of data archiving
145137	27/05/2016	11/08/2016	+76	256	35	26/11/15 to 11/08/16
145142	26/06/2016	12/06/2016	-14	87	1199	17/03/16 to 12/06/16
145143	12/06/2016	28/07/2016	+52	163	123	16/02/16 to 28/07/16
145144	31/08/2016	27/05/2016	-96	38	59	19/04/16 to 27/05/16
145152	30/08/2016	13/11/2016	+75	208	63	19/04/16 to 13/11/16

Interpolated horizontal movements

Interpolated movement tracks for the successfully transmitted inshore ($n = 3$) and offshore ($n = 2$) tagged sea bass (Table 5.3) were provided by CLS and interpreted by the author. Due in part to the magnetometer technology used by the tags to calculate their position, some tag tracks were found to have large 50% and 99% confidence areas. Nonetheless, modelled tracks for inshore tagged specimens suggested periods of migration offshore, corresponding to the reported peak spawning period of April to June.

Table 5.3 Estimated track lengths and maximum linear distance travelled by PSAT tagged fish

PSAT ID	Estimated total track length (km)	Estimated mean distance per day (km/day ⁻¹)	Estimated maximum linear distance from release location (km)
145137	884	3.45	157
145142	674	7.7	89
145143	923	5.56	321
145144	484	12.7	211
145152	1020	4.9	180

Both offshore tagged specimens showed distinct and different track patterns. Fish 145137 (Fig. 5.2) moved in a south-westerly direction during January and February, out of the Bristol Channel and into the open waters of the Celtic Sea. This sea bass then returned towards the Bristol Channel during March and April before moving up into the Irish Sea, crossing St. Georges Channel during the month of May, as it approached the western coast of Wales. The specimen was then estimated to have changed direction, moving south again during June to August, before the late detachment of the tag (76 days beyond the user-defined detachment date) while the fish was off the south-west headland of the Welsh coastline. The mean distance/day⁻¹, based on the estimated track, covered by this sea bass was 3.74km/day⁻¹ which was the slowest mean daily rate of movement recorded during this study.

Sufficient data from fish 145142 were received to produce an accurate track with a comparatively low degree of error (Fig. 5.3). This sea bass, tagged and released in March 2016, travelled in an anti-clockwise loop in the Bristol Channel prior to travelling in a south-westerly direction into the eastern Celtic Sea during April and May. The specimen then changed direction, heading in a south-south-east direction and approached the north coast of Cornwall where it remained, most probably in inshore waters during May and June prior to tag release (which occurred 14 days prior to the pre-defined detachment date). While fish 145142 was estimated to have travelled approximately 647km, the maximum linear distance that this sea bass travelled from its release site was estimated to be 89km.

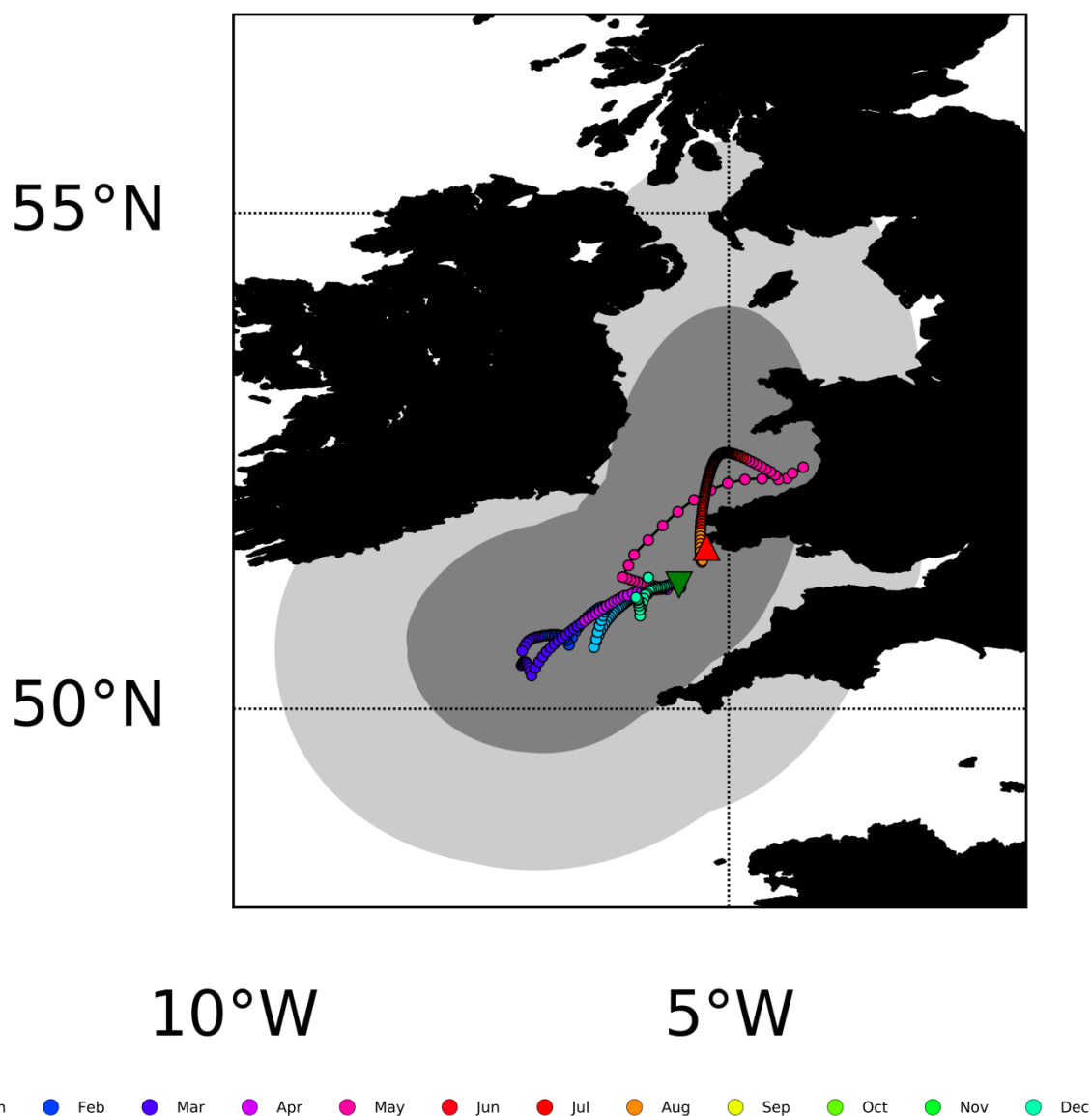
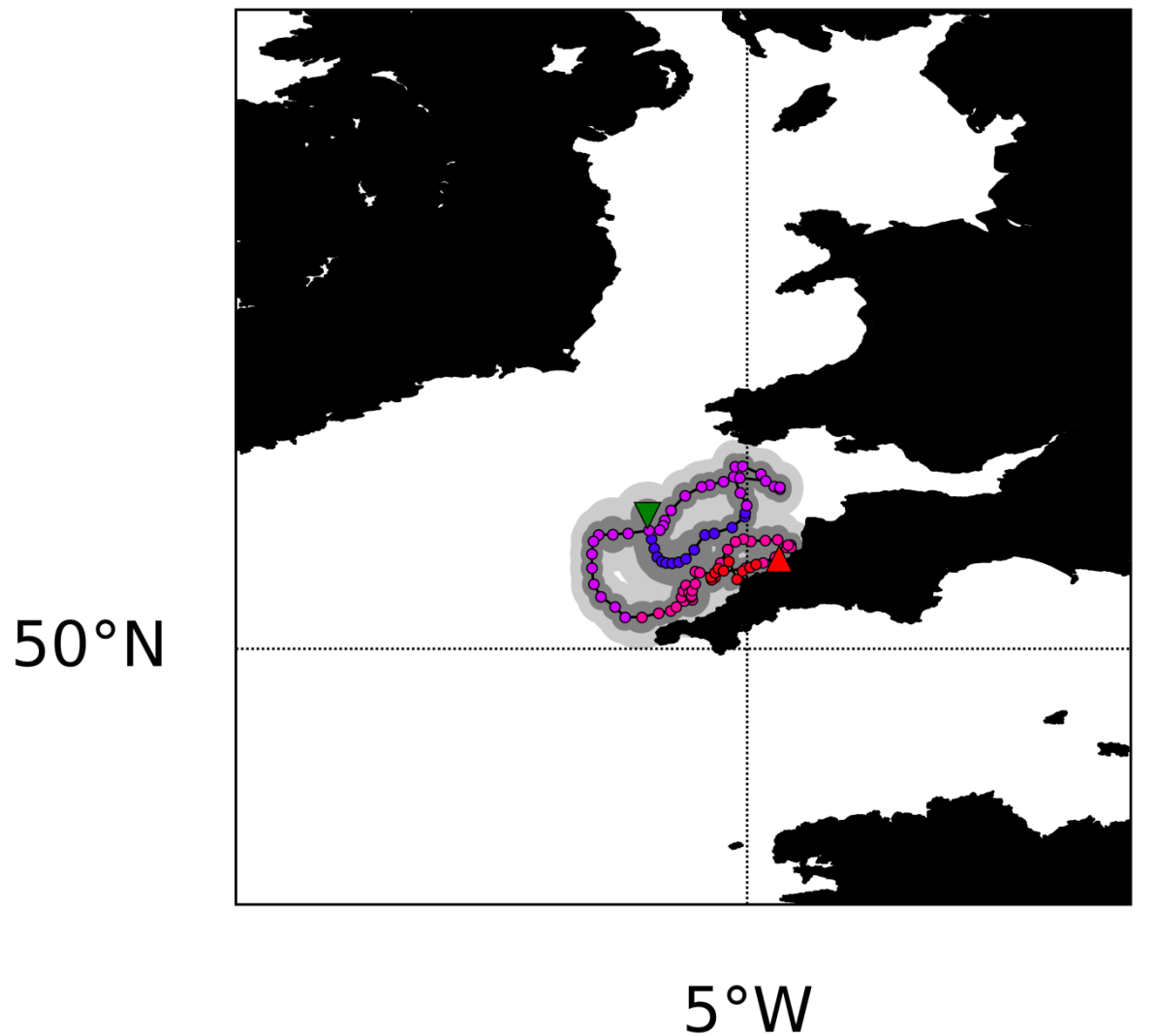


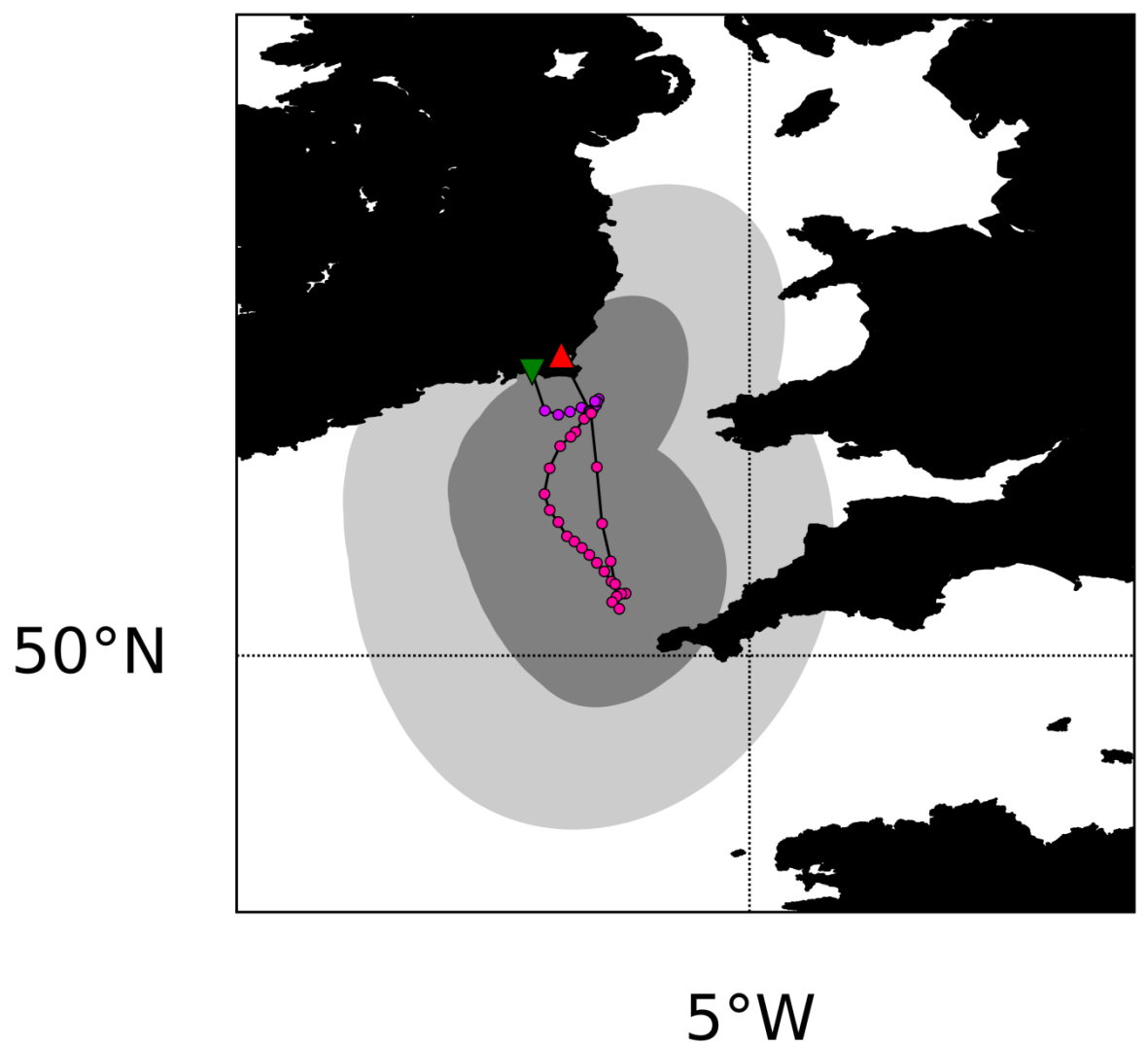
Fig. 5.2 Estimated movement tracks of fish 145137 (dark grey = 50% confidence margin, light grey = 95% confidence margin; release location = green inverted triangle, pop-off location = red triangle) indicated presence in offshore waters in the eastern Celtic Sea during March and April, prior to travelling north-west towards the west coast of Wales in May



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Fig. 5.3 The estimated movement tracks of fish 145142 (dark grey = 50% confidence margin, light grey = 95% confidence margin; release location = green inverted triangle, pop-off location = red triangle) identified its presence within the Bristol Channel prior to migrating out into the eastern Celtic Sea and the back towards the north Cornish coast

The estimated tracks for sea bass which were released from the inshore site in Co. Wexford had large associated areas of 50% and 95% confidence estimates (Fig. 5.4 and 5.5). Data for fish 145144 and fish 145152 suggest that they both migrated offshore during the peak spawning period (May), returning towards inshore waters during the same month. The tag for fish 145144 (Fig. 5.4) detached prematurely (96 days prior to the pre-defined detachment date), 38 days post-release on 27/05/2016. Fish 145144 was estimated to have had the highest mean rate of movement, travelling at a mean speed of 12.7km/day^{-1} based on the estimated track. Fish 145152 (Fig. 5.5) retained its tag up until the 13/11/2016, resulting in a tag retention period of 208 days (75 days after the user-defined release date). Fish 142152 moved north towards the southern Irish coast during June, towards the area where it had been tagged. This sea bass migrated south into offshore waters during August, though again travelled north towards its tagging location during November. It also recorded the highest estimated track length at 1020km while travelling approximately 180km linear distance from its release location. The interpolated tracks of fish 145144 and 145152 display similar characteristics relating to migration direction and timing, showing that they travelled to within approximately 40km of each other at the southern-most point of their migrations, returning to the same approximate area of coastline afterwards. When taking the offshore tagged fish (145137 and 145142) into account also, it was found the tracks of all four sea bass were within 240km^2 of each other within the eastern Celtic Sea.



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Fig. 5.4 Fish 145144 (dark grey = 50% confidence margin, light grey = 95% confidence margin; release location = green inverted triangle, pop-off location = red triangle) made an offshore migration out from the south Irish coast to the eastern Celtic Sea during April before returning to the same relatively discrete region coast again in May

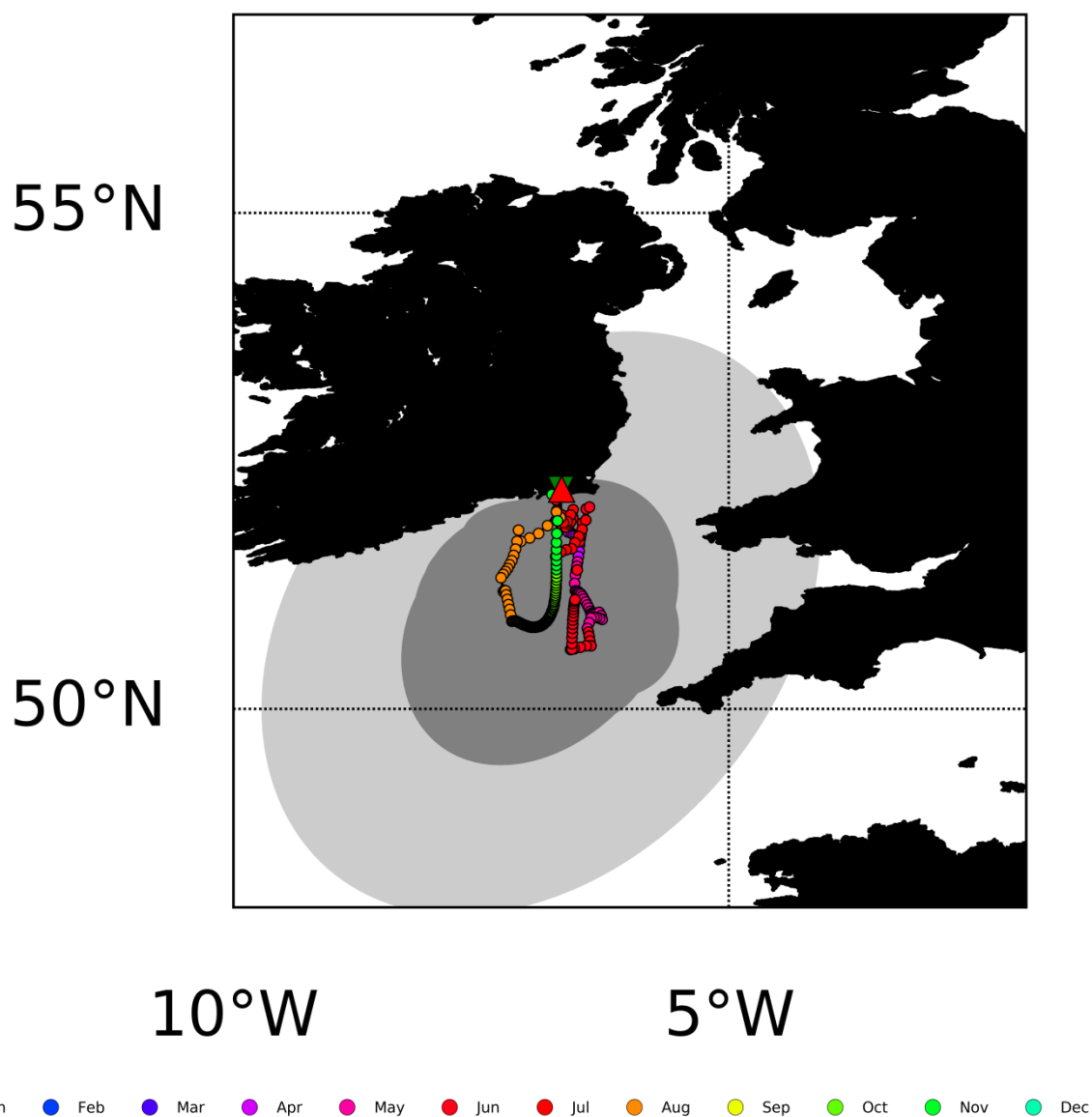


Fig. 5.5 Estimated tracks of inshore tagged fish 145152 (dark grey = 50% confidence margin, light grey = 95% confidence margin; release location = green inverted triangle, pop-off location = red triangle) found that the specimen was present offshore in the eastern Celtic Sea during May and June, after which it travelled back towards the south coast of Ireland. It moved offshore again in August, returning once again to the south coast during October

In contrast to both estimated tracks from sea bass released from inshore waters of Co. Wexford, data obtained from fish 145143, tagged and released in inshore waters of Co. Waterford approximately 20km to the west, showed the sea bass travelling within Irish inshore waters in February and March, migrating around Carnsore Point (south-eastern most point of the Irish mainland) and heading north into the Irish Sea along the eastern Irish coast (Fig. 5.6). This specimen then moved offshore and travelled in a north-easterly direction, crossing the Irish Sea and passing between the Isle of Man and the northern coast of Wales during the months of April/May, travelling an estimated linear distance of 321km from its release location. This sea bass subsequently returned to the southern Irish coast again during June, after which the PSAT detached, having been retained for 163 days (52 days longer than the pre-defined tag detachment setting).

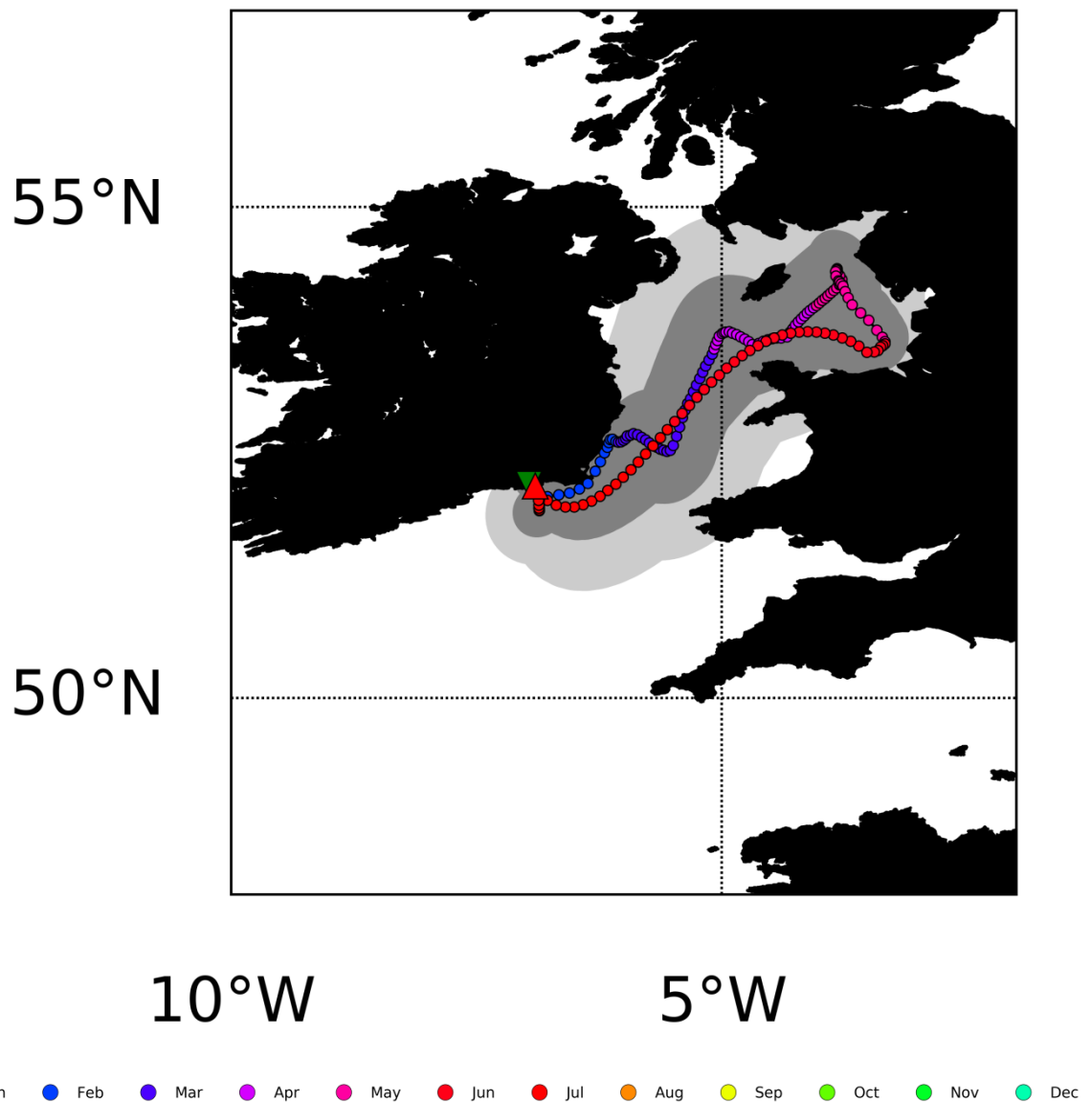


Fig. 5.6 The track of fish 145143 (dark grey = 50% confidence margin, light grey = 95% confidence margin; release location = green inverted triangle, pop-off location = red triangle) recorded migration of the specimen northwards into the Irish Sea during February and March. This specimen then crossed the Irish Sea and was present off the north-west coast of Britain during the assumed spawning period of April and May. This sea bass then returned to the same relatively discrete inshore location in June, to where it had been originally released on the south coast of Ireland

Water temperature results

Tag recorded temperatures were used in conjunction with foundation SST to further refine geolocation. Divergence between these readings may result in the construction of inaccurate tracks. Due to the different deployment times of the PSAT tags and the failure of some tags to record and transmit data, the results for temperature data are widely dispersed, though the majority of data recorded were for the assumed period associated with peak spawning in April, May and June with a mean of 28.3 temperature recordings for each of these months (Table 5.4).

Table 5.4 Mean water temperatures recorded by tagged fish on a monthly basis

Month	No. of temperature recordings	Mean temperature (°C)	+/- SD
Nov-15	1	14.4	0
Dec-15	5	12.14	0.08
Jan-16	1	11.3	0
Feb-16	13	7.6	1.39
Mar-16	25	8.4	0.78
Apr-16	29	9.4	0.87
May-16	31	12.3	1.10
Jun-16	17	15.2	1.22
Jul-16	9	15.9	1.24
Aug-16	7	17.0	1.12

Mean daily temperature readings from the tags during the assumed peak spawning period (April to June) ranged between 7.3°C to 18°C. The mean daily water temperature did not decrease below the 8.5°C threshold after 11 April 2016. The warmest water temperatures were observed in August 2016 (17.0°C) though these data were based on a low number of recordings ($n = 7$) from a single sea bass. The month with the lowest mean temperature recorded was February (7.6°C), which was also found to have the most variable water temperatures, recording the highest standard deviation of +/- 1.39.

Low water temperatures (6.5°C) were recorded by fish 145143 (Fig. 5.8, top) in February during the initial days post-release when the specimen was estimated to still be at the inshore location in which it was released. The recorded water temperature values remained between 6.3°C to 7.9°C during the time that this fish was in Irish inshore waters (February to mid-March) and did not increase above 8.5°C until mid-April, when the specimen appeared to be travelling in a north-westerly direction across the Irish Sea. Data for fish 145137 (Fig. 5.7, top) and 145142 (Fig. 5.7, bottom) shows close correlation between tag-recorded temperature data and satellite observed sea surface temperature (SST), though there are large gaps in temperature data for the fish 145137. Observed temperature was higher than satellite SST in all but one reading for fish 145144 (Fig. 5.8, middle). All specimens, with the exception of fish 145152 (Fig. 5.8, bottom), showed an increase in water temperatures from March onwards. There was significantly higher tag recorded temperatures compared to satellite observed SST values found in fish 145137 (Paired t-test, $t(19) = 5.68$, $p < 0.001$), 145144 (Paired t-test, $t(20) = 8.54$, $p < 0.001$) and 145152 (Paired t-test, $t(43) = 9.7$, $p < 0.001$) while no significant differences were observed in fish 145142 (Paired t-test, $t(80) = 0.38$, $p > 0.05$) and 145143 (Paired t-test, $t(66) = -0.79$, $p > 0.05$).

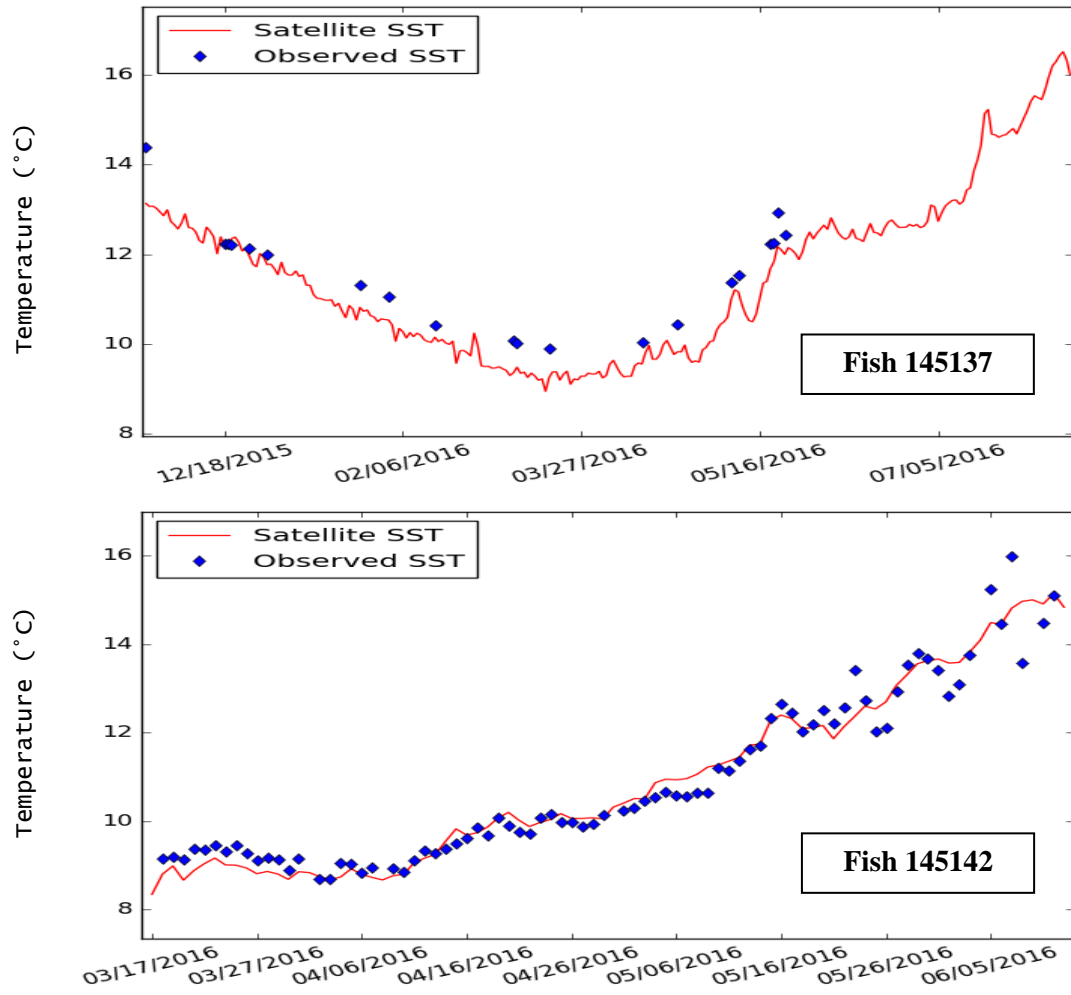


Fig. 5.7 Ambient water temperature recordings (observed) from fish 145137 and 145142 (with additional satellite observed sea surface temperature) saw increases in temperature from late March onwards

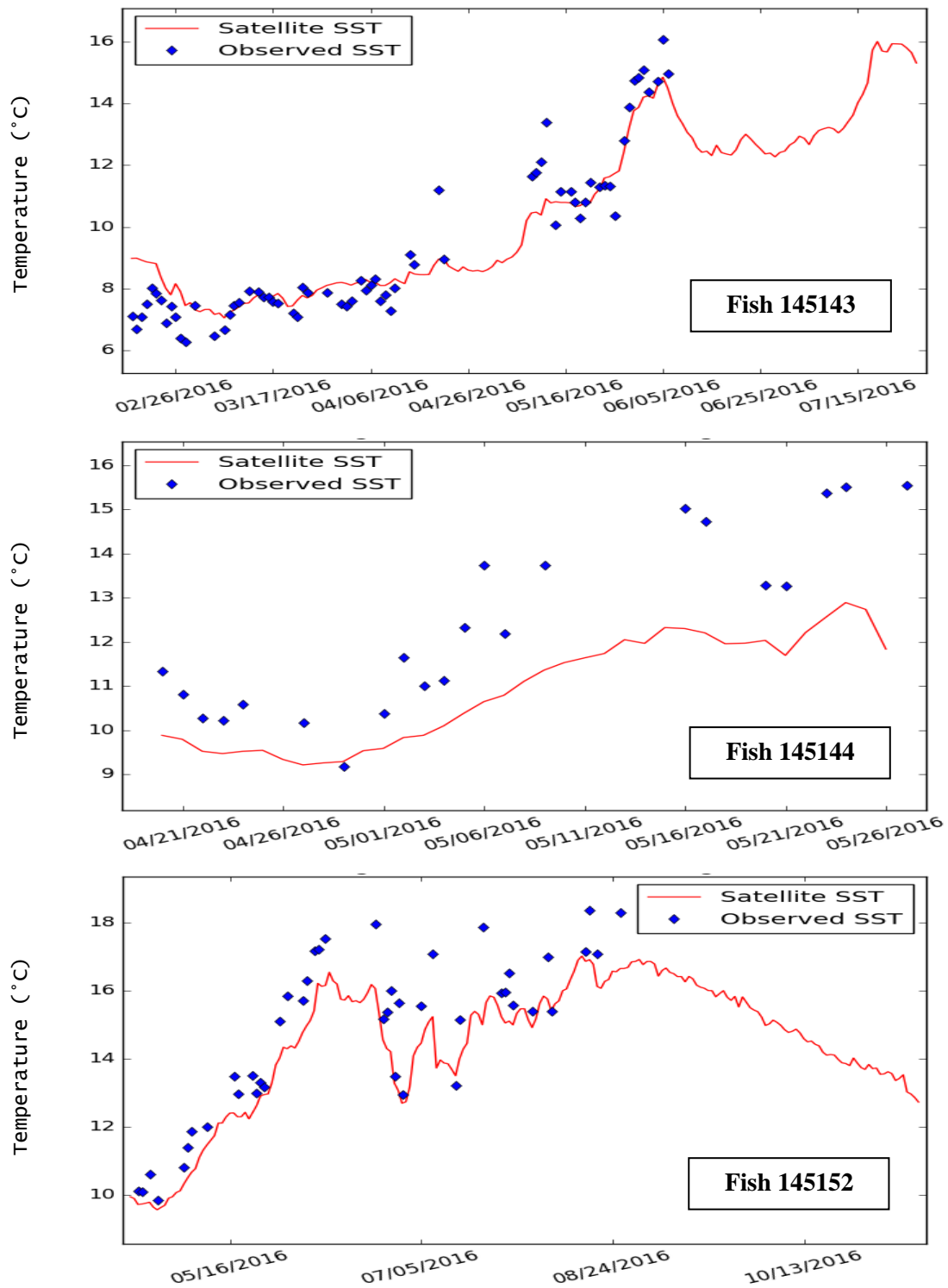


Fig. 5.8 Ambient water temperature recordings (observed) from fish 145143, 145144 and 145152 (with additional satellite observed sea surface temperature). The presence of fish 145143 in inshore waters on the south and east Irish coast is displayed by the lower water temperatures observed during this period

Discussion

This study represents the first reported use of pop-off satellite tags on sea bass. The findings of this study, acknowledging the low sample size and the degree of error in track estimation, indicate that sea bass in Irish waters undertake offshore migrations and that the timing of these migrations do coincide with the assumed spawning period for sea bass, particularly between April and June.

Tag performance and success rate

To date, there have been few studies in which small species (<100cm) of fish have been tagged with PSATs (Graves *et al.*, 2008; Lacroix, 2013; Rodgveller *et al.*, 2017). The SeaTag-GEO PSAT, used in this study, has also previously been used on sable-fish (*Anoplopoma fimbria*), a similar sized fish to sea bass, where a reporting rate of 47% to 58% (Echave, 2016) was similar to that recorded here. The effects of increased drag and swimming effort on the tagged sea bass behaviour and movement are not known, though previous studies on adult Atlantic salmon (*Salmo salar*) found no difference in swimming endurance with small or large external tags attached (Bridger & Booth, 2003). Even though sea bass are a robust species, capable of tolerating low salinities and a wide range of temperatures (Pickett & Pawson, 1994), the impact on swimming speed and the resulting fatigue of having an externally attached tag could be significant, as has been observed in other species such as juvenile bluefin tuna (*Thynnus thynnus*), Atlantic cod (*Gadus morhua*) and European plaice (*Pleuronectes platessa*) (Arnold & Holford, 1978; Hoolihan *et al.*, 2011; Jepsen *et al.*, 2015). The considerable distances and mean daily rate of movements recorded in the sea bass in this study however, would suggest that the presence of the PSAT did not adversely affect the migratory ability of the tagged specimens.

The failure of seven of the tags in this study to detach and transmit data may be attributable to a number of factors. Sea water infiltration may have destroyed the PSAT electronics (Abascal *et al.*, 2016), with the additional possibility that the charging powder to allow for tag detachment may have become dampened, preventing release of the tag. The physical failure of the bridal system or detachment through inadequate tissue healing was assumed responsible for the premature detachment of one PSAT (145141), which shed one day post-deployment despite no ‘detach’ command being received. Impact damage from the high energy environments that inshore sea bass are typically found in, such as around reefs or in surf zones, may have also contributed to the below average successful reporting of deployed tags, with breakage of tag aerals potentially limiting data recovery (Hays *et al.*, 2007). In particular, given the foraging nature of sea bass, it may be possible that some un-reported tags had become stuck in weed beds underwater (Bridger & Booth, 2003) or lodged in cracks or caves on the sea floor (Jepsen *et al.*, 2015). It may also be possible that some tagged specimens were caught commercially, with the PSATs retained to obscure the location of fishing grounds and fishing activity as suggested by Hays *et al.*, 2007. The delayed pop-off of three of the five tags in this study may have also been due to possible technical issues with the tag hardware or software, preventing the tags from adhering to the user-defined pop-off dates.

The accuracy of the PSATs used in this study was found to vary considerably. Only fish 145142 was found to have a relatively accurate track while other tagged fish data, notably fish 145144 and 145152, was found to be less accurate, resulting in a more uncertain track prediction. The use of the magnetometer, in conjunction with light levels, for geolocation may be a source of this discrepancy. The existence of a magnetic anomaly, comprised of a line of iron-rich rock bodies, stretching from the southern coast of Co. Wexford, Ireland to the northern Anglesey coast in Wales, UK (Wonik *et al.*, 2001) in addition to the presence of sunken shipwrecks in the vicinity of the release area, particularly for inshore tagged

specimens (INFOMAR, 2017), may have reduced the effectiveness of the magnetometer thereby reducing estimated track accuracy (Desert Star Systems, 2016). The future use of PSATs on fish likely to migrate within this specified area should take these factors into account, perhaps employing the use of light and temperature based tags for geolocation as a potentially more reliable alternative.

Estimated horizontal tracks

The estimated tracks of inshore tagged fish 145144 and 145152 imply that both sea bass were present in the eastern Celtic Sea during the peak spawning period (April to June), thus suggesting behaviour indicative of a spawning migration. The offshore tagged specimens (145137 and 145142) were also present in the eastern Celtic Sea during the same period, before subsequently migrating eastwards towards inshore areas on the western British coast, suggesting that these sea bass may have originated from there (Kelley, 1979; Pawson *et al.*, 1987). The inshore tagged sea bass (145144 and 145152), having travelled offshore in a southerly direction from the south-east Irish coast, returned towards the coast where they were tagged, suggesting that they may be sea bass originating from nurseries on the Irish coast.

While the origin of these sea bass may differ, they migrated to the same approximate area in eastern Celtic Sea (within 240km²) during the spawning season (Fig. 5.9), suggesting a possible aggregation of spawning sea bass at this location. Tracks from fish 145152, 145137 and 145144 all overlapped while migration routes of offshore tagged fish, 145137 and 145142, also overlapped. At their closest points, all specimen tracks, with the exception of 145143, were separated by approximately 40km from each other in the eastern Celtic Sea in the period between April and June. It is unlikely that any of these four sea bass migrated south of the Cornwall/Devon peninsula, entering into the Western Approaches and English

Channel. Preliminary results from the use of data storage tags (DST) to track sea bass movements has also revealed migration of sea bass from the English Channel to the eastern Celtic Sea, though research is still ongoing (CEFAS, 2016). The interconnectivity between spawning aggregations within these separate areas is unknown, though there is some suggestion that sea bass from the western coast of Britain do enter the English Channel, having been previously reported in French inshore waters (Kelley, 1979; Pawson *et al.*, 1987).

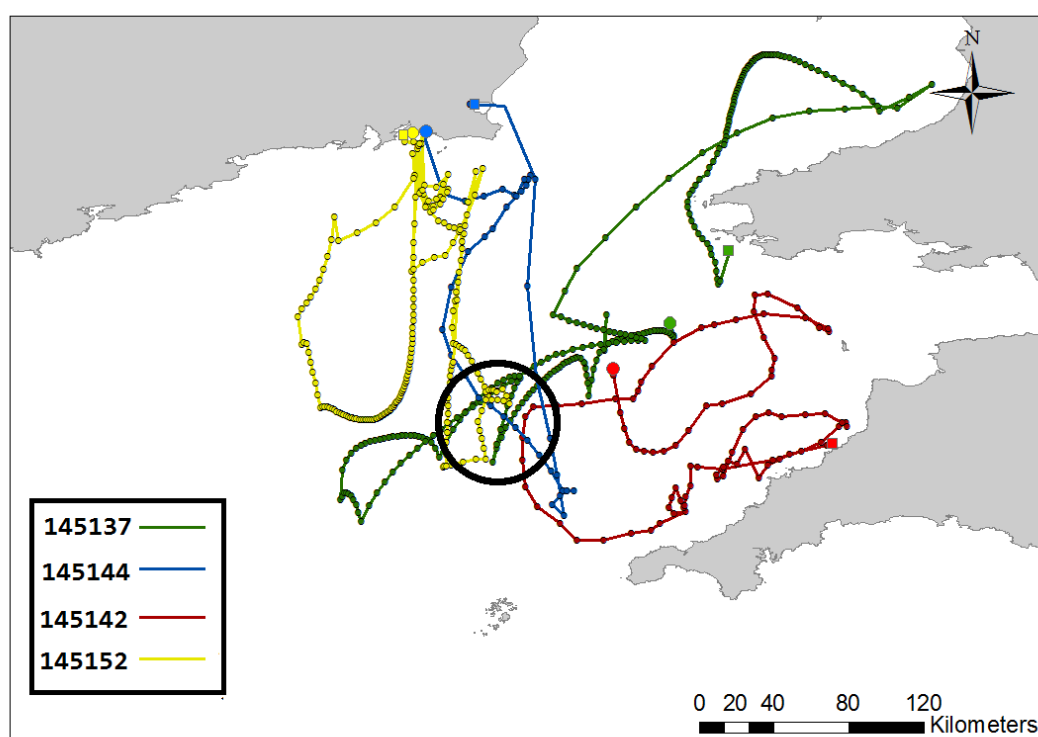


Fig. 5.9 Interpolated tracks from fish 145137, 145142, 145144 and 145152 showed evidence of aggregation (black circle) in the eastern Celtic Sea between April and June

Fish 145143, tagged in inshore waters on the south Irish coast, appears to have travelled in a substantially different to the other tagged specimens in this study. This specimen travelled from the south Irish coast to the waters off the north-western England, within Liverpool Bay. The result and the reported northward migration of sea bass on the west coast of Britain (Kelley, 1979) during this peak spawning period therefore, may suggest that sea bass may

also spawn in this area. Further evidence of migration of sea bass of Irish origin to this location was recorded in November 2016 when a floy tagged specimen was recovered in Morecambe Bay, having being released in April 2016 in south-east Ireland (Marine Institute, unpublished). Annual demersal surveys undertaken by the Agri-Food and Biosciences Institute (AFBI) have identified the presence of sea bass at offshore locations in the northern region of the Irish Sea during November, when it is assumed that adult fish are in a pre-spawning stage (see Chapter 2).

Evidence of the return migration to relatively discrete inshore locations on an annual basis by adult sea bass has been noted in tag/recapture studies, with some sea bass being recaptured at the same location on a year-on-year (Pawson *et al.*, 2007). However, the findings presented here show the first strong evidence of sea bass offshore migration and return to their location of tagging and possibly its inshore coastal native nursery and feeding area. All three inshore tagged specimens returned to within approximately 73km of the location in which they were released. Both offshore sea bass also were also observed to move into inshore waters but as they were tagged offshore, it is impossible to ascertain whether they migrated back to their nursery zones.

Water temperature results

Migration of sea bass southwards on the western British coast has been found to coincide with decreasing water temperatures at the end of autumn and start of winter (Kelley, 1979; Pawson *et al.*, 1987). These migrations are believed to be linked to reproductive behaviour, which has a strong correlation with ambient water temperatures above 8.5°C (Thompson & Harrop, 1987; Pickett & Pawson, 1994). Pawson & Pickett (1996) also suggested that sea bass which remain in warmer offshore waters throughout the winter experience a growth advantage compared with those which stay in shallower, cooler inshore or more northerly

waters. In this study, mean water temperatures recorded by the PSATs were found to be above the threshold of 8.5°C from April 11th to the end of June suggesting that spawning may have occurred during this period.

While declining water temperatures in the Irish Sea were thought to initiate the movement of sea bass south during autumn and winter, northward migration of sea bass has been observed in previous studies during summer time as water temperatures increase again (Kelley, 1979). The recorded movement track of fish 145143 corresponds with this pattern, although the specimen left the southern Irish coast to travel to the north-west coast of England before it returned to the southern Irish coast after this period. While water temperatures did increase in the Irish Sea between April and June, they were relatively cool, while corresponding temperatures in the Celtic Sea were observed to be warmer (Fig. 5.10). This therefore poses the question as to why this sea bass migrated in a northerly direction? It may be possible that this sea bass was migrating to spawn in the warmer, nearshore waters off the coast of Morecambe Bay, which were recorded in May (Fig. 5.10, middle), than in the cooler waters found along the south Irish coast. The specimen's presence in the waters off the north-west English coast coincided with an increase in observed temperature recordings from the PSAT during the same period (Fig. 5.8), with the elevated water temperature allowing for increased larval survival and development (Pickett & Pawson, 1994).

The extent of spawning migration undertaken by sea bass has also been found to vary in accordance with prevailing climatic conditions (Kelley, 1979). Warmer, milder winters are thought to result in adult sea bass remaining in inshore waters for longer while also migrating shorter distances in order to spawn, while colder autumnal and winter periods may result in longer migration periods to areas of warmer water (Kennedy & Fitzmaurice, 1972; Holden & Williams, 1974; Pawson *et al.*, 2007). As a result, the location of spawning sites and the migratory pathways for sea bass might be assumed to be dynamic, with the presence of optimal water temperatures assumed to be the primary influence on their location.

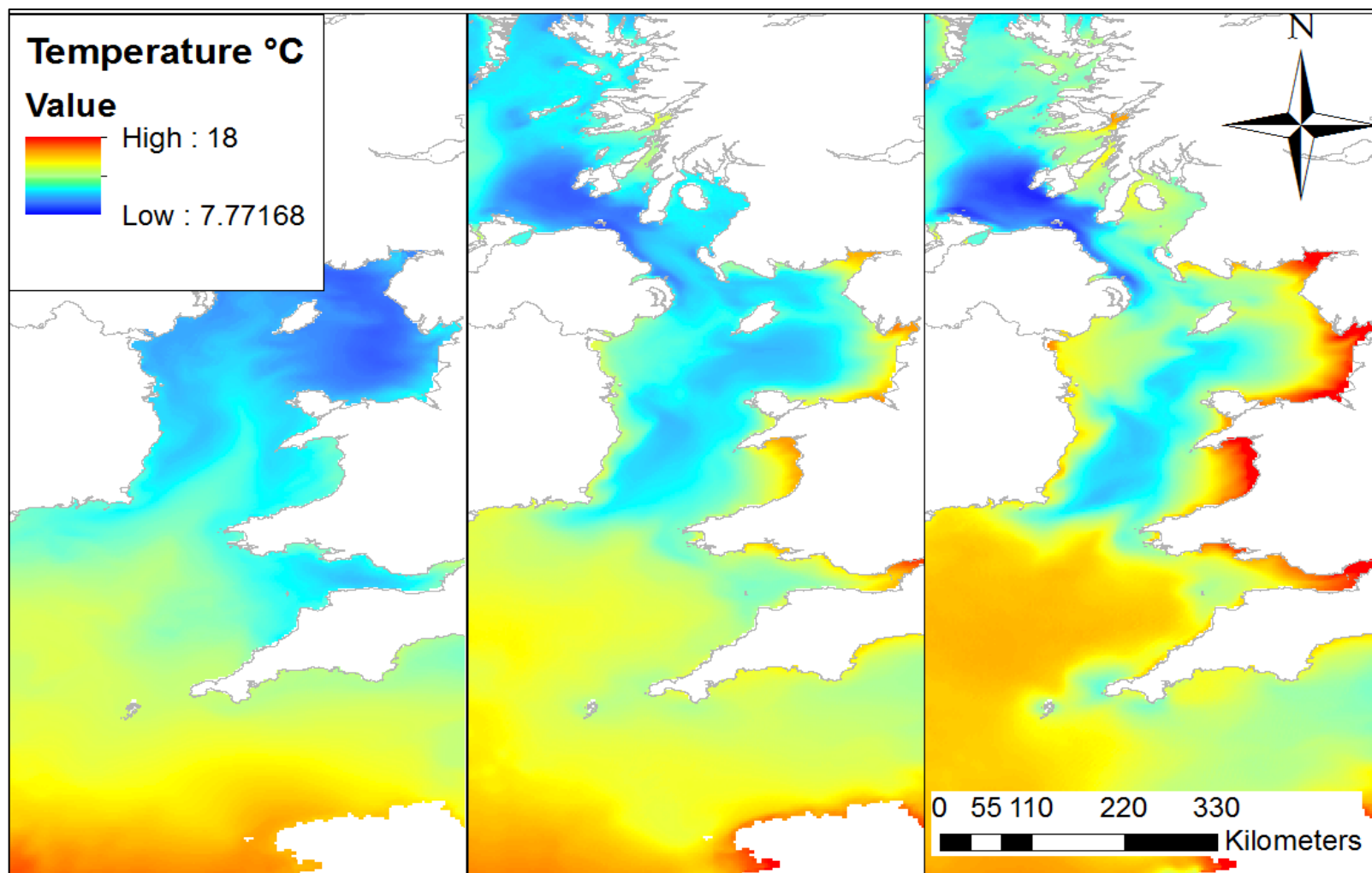


Fig. 5.10 Mean monthly modelled sea surface temperatures for April (left), May (centre) and June (right) 2016 show evidence of warmer waters in the Celtic Sea when compared to the Irish Sea (Source: Marine Institute – URL: <http://data.marine.ie/Dataset/Details/20956>)

Potential management implications

Kennedy & Fitzmaurice (1972) concluded that sea bass within Irish waters spawned inshore, often in areas close to large river estuaries. More recent information, based on acoustic tracking, showed that a proportion of acoustically tagged sea bass (28.9%; $n = 11$) did remain resident in inshore Irish waters along the south-east coast during the spawning season from February to June, 2016 (see Chapter 4). This may suggest possible inshore spawning as according to Kennedy & Fitzmaurice (1972), sea bass will spawn every year once mature. However, additional acoustic data suggested that 21 of the 23 non-resident fish were absent for consecutive periods of 20 days or more during the assumed spawning period (February to June) and were therefore capable of migrating to offshore spawning grounds. The data obtained from the inshore PSAT tagged specimens in this study also suggests offshore migration during this same period, both into the Celtic Sea and Irish Sea. This suggestion is in accordance with the findings of sea bass larval research undertaken by Thompson & Harrop (1987) in British waters which concluded that while sea bass spawning did occur inshore, that the majority of the activity occurred offshore. While this may imply that spawning by sea bass of Irish origin may potentially occur in both inshore and offshore waters, no ichthyoplankton surveys to date have identified the presence of sea bass eggs and larvae in offshore Irish waters (see Appendix 3.0).

Though confirmation of the behaviour of sea bass larvae in the wild is still unknown, modelled simulations, based on diel vertical migration and passive behaviour, have shown that larvae released from offshore locations in the Celtic Sea could be potentially transported into inshore waters and related nearby nursery habitats such as lagoons, backwaters and estuaries (see Chapter 3). The interpolated tracks suggest the potential existence of an offshore spawning site in the eastern Celtic Sea which, though already identified for sea bass of British origin, may also be an offshore spawning location for sea bass originating from

Irish waters. The migration of fish 145143 to the north-west British coast may also be evidence of aggregative behaviour, and possibly spawning, with sea bass originating from British inshore waters. Should Irish and British sea bass spawn in the same location, it would be strong evidence that they may be part of a single panmictic group of interbreeding individuals and could therefore be considered part of the same genetic population. This may have significant implications regarding the management of sea bass in the Celtic Sea region, given their ability to cross into various jurisdictions and management areas.

Previous to this study, there was no evidence of interconnectivity between sea bass stocks between both countries (Kelley, 1979; Pickett & Pawson, 1994), with the exception of a single specimen documented in Pawson *et al.* (2007). While mixing of sea bass originating from Irish and British inshore waters at offshore locations in the Celtic Sea had previously been suggested (Fahy *et al.*, 2000), the migratory routes of sea bass between both countries was unknown apart from a single specimen originally tagged in inshore Irish waters, which was recaptured 60km off the south-east coast of Ireland three weeks post release (Pawson *et al.*, 2007). While the fidelity to inshore nursery and feeding locations observed in the three fish released from Irish inshore waters is also in accordance with previously reported behaviour (Pawson *et al.*, 2007), the interpolated migration tracks provide further evidence of the extent that sea bass will travel. It has been suggested that the small-scale of sea bass fisheries operating in Ireland prior to 1990 and the closure of the fishery since (IFI, 2014) has contributed to these poor levels of tag returns. This may have enhanced the impression that sea bass populations in Irish waters were “essentially local” (Holden & Williams, 1974) and were not part of a larger aggregation of fish which spawned in the south-east Celtic Sea. The findings of this study however, do suggest that both Irish and British sea bass stocks are interconnected, though the extent is still unknown.

Conclusions

The location of sea bass spawning grounds in British waters has been well documented (Dando & Demir, 1985; Thompson & Harrop, 1987; Jennings & Pawson, 1992). In contrast, the spawning locations of sea bass frequenting Irish waters have never been identified conclusively. The findings of this study suggest that it is likely that a proportion of sexually mature adult sea bass in Irish waters migrate from the southern Irish coast to spawn in the eastern Celtic Sea and north-west Irish Sea during the assumed peak spawning season between April and June. The extent to which these sea bass travel may vary on an annual basis, if related to water temperature or prey availability, but track outputs suggest that Irish sea bass may spawn in around the same area and time as those that originate on the west coast of Britain and in the eastern Celtic Sea.

Based on the results of this study, the use of PSATs as a method of tracking sea bass movements in offshore waters is a viable method capable of providing new insights into the migratory behaviour of the species. However, there are still unanswered questions about sea bass migration, particularly concerning the method by which fish can identify their inshore nursery/feeding sites when returning from their post-spawning migration. Given the limited sample size, further research is required to substantiate these findings and to establish a more definitive picture of the level of interconnectivity between sea bass stocks in Ireland and Britain.

Acknowledgements

The author was supported by the Beaufort Marine Research Award in Fish Population Genetics funded by the Irish Government under the Sea Change Programme and by funding received directly from the Marine Institute. Further acknowledgments are due to Dr Tom Murphy, Nigel Bond and Deirdre Cotter for their assistance in fish handling and surgical

techniques. The author would also like to thank the various Marine Institute staff who assisted with field work including Joe Cooney and Dermot Fee among other. Finally, the author would like to acknowledge the assistance of Sean Rooney (Bass Fishing Wexford), Jim Hendrick (Pro-Bass Fisher) and Cian O'Halloran (Absolute Fishing) in providing local knowledge to allow for specimen acquisition.

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Chapter 6

General discussion

General discussion

In this thesis, some of the key aspects of previously unknown sea bass biology in Irish waters have been investigated, the findings of which will have implications for conservation strategies of sea bass stocks in Ireland and further afield. There has been a sharp decline in sea bass stocks across Europe in recent years, culminating in a ban on commercial and recreational exploitation between January and June of 2016 as per EC Council Regulation No. 2015/259 (EC, 2016). A decrease of total allowable catch (TAC) for sea bass across European waters of over 90% from 6000 tonnes in 2009 to 541 tonnes in 2015 (ICES, 2015) further highlights the pressure on stocks. In addition, there is also concern regarding contemporary levels of spawning stock biomass.

Though commercial exploitation of sea bass in inshore Irish waters ceased in 1990 (IFI, 2014), there is still a large targeted recreational fishery operating, principally conducted by French and British fishermen. As there is only a partial seasonal closure for fishing in European waters, commercial fishing continues outside this period, including in areas in close proximity to Irish inshore territorial waters. Understandably, as a result of French and British boats landing sea bass, Irish commercial fishermen are also anxious to gain access to the sea bass fishery. These fisheries potentially impact negatively on the Irish inshore recreational fishery. A recent report based on a survey of anglers estimated that the sea bass fishery in Ireland was valued at approximately €81 million annually to the economy (Hynes *et al.*, 2017) with anglers travelling from other European nations such as Britain, France and Belgium. The net result of this current management situation is that sea bass fisheries are controversial and contested. The exposure of sea bass stocks in Irish waters to exploitation, whether recreational or commercial, is a function of their biology and specifically their life history. A sea bass stock that spawns in Irish inshore waters and lives its entire life within the confines of local bays, estuaries and lagoons is unlikely to be troubled by the activities of offshore commercial fleets, but would be more sensitive to pressure from recreational angling

or possibly by-catch in other Irish inshore fisheries. In contrast, the productivity of a stock that depends on recruitment from fish that reproduce as part of an offshore aggregation would be sensitive to commercial fishing.

As there is only limited knowledge for fisheries management to employ an investigation of sea bass biology in Irish waters, it is therefore timely to increase the understanding of the species biology, distribution and spawning behaviours. This new information will allow fishery managers to work towards creating management plans to provide a sustainable fishery and to protect and conserve sea bass within Irish waters, particularly given their economic importance.

The origin of sea bass in Irish waters and in the Celtic Sea

Based on the findings of the studies reported in this thesis, it is apparent that a substantial aggregation of sea bass occurs annually in the eastern Celtic Sea (Chapter 2). I believe that the distribution of this aggregation is of a greater geographical extent than was previously thought, extending from the waters of the Bristol Channel across to the south coast of Ireland. The consistent annual catches by the IGFS suggest that there has been little variation in observed geographical distribution of sea bass presence offshore during the 2003 to 2015 period. In addition, the similarities in observed biological traits compared with those reported in central and northern regions (Welsh coast and Bristol Channel) by Pawson & Pickett (1996), further supports the idea that this represents the early formation of a single trans-Celtic Sea spawning aggregation, which will reproduce in this approximate area during the following spawning season. Based on analysis of simulated larval dispersal models (Chapter 3), it is reasonable to assume that this aggregation could also be a source of juvenile sea bass recruitment into Irish coastal waters.

The Celtic Sea spawning aggregation appears to be a mixture of fish originating from both Irish and British nursery areas (Chapter 5), and potentially from other regions. The long-range migratory behaviour of sea bass documented in Chapter 5, shows that sea bass can travel to spawning grounds substantial geographical distances away and that gene flow over large distances is therefore likely.

Previous tagging and genetic studies on sea bass suggest that while movement between populations of fish found in Irish coastal waters and other regions within Europe and Britain is evident, the extent to which this occurs is likely to be negligible (Kennedy & Fitzmaurice, 1972; Kelley, 1979; Fritsch *et al.*, 2007). Genetic studies by Fritsch *et al.* (2007) also suggest the existence of a sub-population of sea bass off southern Ireland. In contrast, however, Coscia & Mariani (2011) found that sea bass in Irish waters were part of a single population in the Celtic Sea which incorporated sea bass from the south coast of Ireland and the west coast of Britain.

Using the samples collected in my various studies (Chapter 2, Chapter 4 and Chapter 5), the result of a small scale genetics study undertaken in this thesis with Queen's University Belfast (Appendix 4.0) appears to support the findings of Cosica and Mariani (2011). This indicates strongly that sea bass from inshore Irish waters and from offshore waters in the Celtic Sea are part of the same panmictic population. Interestingly, an out-sample collected from the North Sea also suggested that sea bass occurring there were genetically very similar to specimens sampled in Irish coastal and offshore waters.

It is reasonable to conclude that the aggregation of sea bass at offshore locations in the Celtic Sea (Chapter 2 and Chapter 5) may imply interbreeding of individuals originating from nursery zones in Irish and British inshore waters potentially those of other regions. The lack of significant genetic diversity reported between inshore and offshore samples, in addition to samples from the southern North Sea, further supports the suggestion that sea bass which

originate in Irish waters are part of a larger single population, incorporating sea bass from the Celtic Sea and North Sea.

The observed genetic homogeny may be primarily due to two factors. The first factor concerns the movement of genetic migrants and gene flow between different geographical locations. Over time, this process may account for the lack of significant genetic variation. While there is evidence of inshore residency of sea bass in Irish waters (see Chapter 4), the findings of Naciri *et al.* (1999) suggest that a small number of genetic migrants can result in genetic homogeny between populations. While it might be assumed that the geographical separation of sea bass in the North Sea and those found in Irish inshore waters and offshore in the Celtic Sea may restrict migration between these regions (Naciri *et al.*, 1999), sea bass have been documented to migrate over considerable distances. Sea bass tracked using pop-off archival tags (PSATs) were recorded travelling over 480km in 38 days on spawning migrations (see Chapter 5) while Pawson *et al.* (2007) reported another specimen, tagged in the English Channel, recaptured over 1200km away, in the south of the Bay of Biscay, just two months after release.

Another possible source of gene flow between the three regions investigated in this genetics study is the mixing of pelagic larvae in common offshore spawning grounds. The aggregation of pre-spawning sea bass in the Celtic Sea has been documented on annual surveys carried out in early winter by the Marine Institute (see Chapter 2). Additionally, interpolated migration tracks from sea bass tagged with PSATs have strongly suggested that sea bass from both Irish and British origins aggregate, or at least coincide spatially and temporally, in a common spawning location in the eastern Celtic Sea and in the north-west Irish Sea during the assumed peak spawning period between April and June (see Chapter 5). It is possible, given the documented migration distances, that sea bass originating from North Sea inshore nursery zones may travel to the Celtic Sea to spawn, resulting in the mixing of larvae from all three regions. Sea bass tagged with data storage tags (DST) by CEFAS have recorded

movements of adult sea bass out of the English Channel and into the Celtic Sea during the assumed spawning period, with evidence of post-spawning migration back towards the North Sea (CEFAS, 2016). Synchronised spawning in sea bass from these stocks at a common spawning location would therefore result in a mixing of pelagic larvae as they are dispersed into coastal nursery zones on Irish and British coasts.

The combination of both larval mixing and genetic migrants between sea bass originating from the three regions could therefore account for the genetic homogeneity observed and also for the lack of stock structure within the offshore samples. I therefore believe that due to the combination of these genetic analysis results, in conjunction with the behavioural similarities observed in sea bass in both inshore and offshore Irish waters compared with other regions in Europe, it can be stated that there is no longer any discernible reason to differentiate “Irish sea bass” from their counterparts across in Britain and potentially further afield.

Evidence for inshore and offshore spawning in sea bass in Irish waters

The results of the biotelemetry approaches used in this research (Chapter 4 and 5) have provided evidence for the possibility of both inshore and offshore spawning of sea bass in Irish waters. Inshore residency was identified in 11 tagged sea bass over the assumed spawning period in Chapter 4, which may be an indication of inshore spawning, as previously suggested by Kennedy & Fitzmaurice (1972). The utilisation of such a spawning strategy may result in increased local retention of larvae in local eddies or gyres. The larval dispersal model output from putative inshore spawning areas on the south-east Irish coast suggest that such inshore spawning could result in recruitment of sea bass as far away as the south-west Irish coast, over 200km away (Chapter 3). I also speculate in Chapter 4 that the residency behaviour exhibited by these 11 fish may not be associated with inshore spawning, but may be as a result of poor conditioning and, as a consequence, a failure to mature in that year,

which would therefore result in the sea bass not initiating migration to offshore spawning location. This could be interpreted as potential evidence of skipped spawning. Life-history theory suggests that fish may skip reproductive events after initial maturation to maximize lifetime fitness and there is robust evidence for this in other species such as Atlantic cod (*Gadus morhua*). Additionally, warmer temperatures in inshore waters during winter may delay spawning migration, resulting in an increased possibility of inshore spawning.

It is more likely however, that the majority of sea bass spawn offshore, as Thompson & Harrop (1987) concluded for sea bass in British waters. While an exploratory larval survey in April 2016 failed to identify the presence of sea bass eggs or larvae in Irish inshore waters or in the Celtic Sea (Appendix 3.0), the discrete distribution of sea bass identified on the IGFS (Chapter 2), in addition the periods of consecutive absences during the assumed spawning season for acoustically tagged fish (Chapter 4) and the offshore aggregation of sea bass observed from PSAT data (Chapter 5), strongly suggest that sea bass originating from Irish waters spawn offshore. It is likely that these fish spawn in the same offshore locality as sea bass originating from British waters with both telemetry results (Chapter 5) and genetic analysis (Appendix 4.0) suggesting a common spawning ground and mixing of pelagic larvae. While larval dispersal may vary based on a spatio-temporal basis, simulations show that particles representative of sea bass larvae released from potential spawning locations in the Celtic Sea are transported towards Irish inshore waters on the south coast (Chapter 3). There is also evidence from the modelling output (Chapter 3) that spawning in the mid-Irish Sea may result in the dispersal of larvae as far north as the north coast of Ireland and as far as the south coast of Scotland.

Spawning aggregations of sea bass may therefore potentially act as larval sources for areas separated by considerable geographical distances. The viability of both inshore and offshore spawning scenarios as sources of recruitment for sea bass in Irish waters was shown to be plausible based on theoretical simulation (Chapter 3). The far-reaching effects of sea bass

larval dispersal further highlight the importance of protecting spawning aggregations in both inshore and offshore waters and this point must be taken into account by fishery managers when compiling stock management plans.

Site fidelity of sea bass in inshore Irish waters

The repeated use of discrete inshore locations by adult sea bass on an annual basis has previously been reported in British waters (Pawson *et al.*, 2007), providing evidence that the same site can be used repeatedly, and revisited even after absences of some months. The use of biotelemetry in this project, however, has provided more insight into the repeated use of single inshore feeding/nursery sites or areas by sea bass (Chapter 4) and is in accordance with the newly published findings of Doyle *et al.* (2017). The majority of tagged sea bass were only detected within the study area on receivers located a short distance (0-5km) away from where they were released, suggesting a relatively local area usage for prolonged periods of time or repeat periods. The low level of migration between inshore sites within the study area, in addition to the return of tagged sea bass which had been absent during winter and spring months, confirm that sea bass will use the same local site regularly. The behaviour of PSAT tagged specimens also confirms this behaviour (Chapter 5).

The high level of site fidelity reported in this study emphasises the fact that while sea bass do move between inshore locations, and the majority likely move offshore to spawn, stocks in inshore waters may be considered “local” for the purposes of local fisheries management. This is due to a high degree of association with a particular site or area and results in the sea bass being particularly vulnerable to persistent exploitation or catch and release fishing. Potential local by-laws should reflect this behaviour to allow for maximum protection from growth overfishing of older, larger fish, on which the success of the current recreational fishery is founded and continues to rely on.

Future research recommendations

While the findings of my research displayed in Chapters 2, 3, 4 and 5 may establish a new baseline concerning sea bass distribution and biology in Irish waters, it is important to build on this knowledge. The biotelemetry data highlighted in Chapters 4 and 5 provides an insight into the migratory patterns of sea bass in both inshore and offshore Irish waters. From a fisheries management perspective, these findings have important implications. However, it is important to note that changes within the marine environment may affect these behaviours over time (Miah, 2015; Muhling *et al.*, 2011). The uncertainty of the impacts of climate change may also have a significant influence on sea water temperatures, which are believed to effect the location of offshore spawning areas on an annual basis (Thompson & Harrop, 1987; Pickett & Pawson, 1994). As such, it is recommended that further research should be undertaken to investigate changes in sea bass distribution over a longer time period, with a focus on environmental influences. This could be achieved through the use of biotelemetry but also through large scale tag/recapture programs, conducted in a collaborative manner between Ireland and Britain.

The clustering of sea bass catches (Chapter 2) and the apparent aggregation of sea bass in assumed spawning locations in the Celtic Sea (Chapter 5) has provided evidence for the identification of putative offshore spawning areas. Additionally, the residency of some tagged sea bass within the study area for the duration of the assumed spawning season (Chapter 4), may also suggest the possibility of inshore spawning. Temporal larval surveys, similar to that undertaken in Appendix 3.0, are therefore recommended at both inshore and offshore locations to confirm the occurrence of spawning within these areas. Knowledge of sea bass larvae behaviours in the wild and potential transport routes to inshore nursery zones can be used to increase the accuracy of modelling simulations, such as those in Chapter 3, for predicting larval dispersal in future years.

While genetic analysis revealed that sea bass from Irish inshore waters and those found offshore on the west coast of Britain may be part of the same panmictic population, site fidelity was apparent in sea bass in inshore waters (Chapter 4 and 5). The limitations of acoustic biotelemetry however, make the investigation of the localisation of inshore feeding stocks within inshore regions difficult. It is therefore recommended that stable isotope analysis be undertaken on sea bass from coastal regions around Ireland to identify evidence of localisation based on regional feeding behaviours, similar to the research undertaken by Cambie *et al.* (2016) in Welsh coastal waters. Knowledge of regional inshore feeding stocks could allow fishery managers to develop optimal management plans for sea bass conservation in inshore waters.

Management considerations

The evidence presented here points overwhelmingly to sea bass occurring in Irish waters as being an integral part of the larger trans-Celtic Sea population. That is:

1. The existence of a separate “Irish” population of sea bass is unfounded and th
2. The previously recognised Bristol Channel spawning aggregation extends westwards towards the south coast of Ireland
3. That particle tracking output shows that sea bass larvae can be delivered along the Irish coastline, particularly along the south coast, from both inshore and offshore locations
4. That consecutive long absence periods for two thirds of the acoustically tagged fish in inshore waters, concurrent with the assumed spawning period, may suggest substantial offshore migration to spawning aggregations

5. Data from PSAT tagged specimens suggests that at least some sea bass that originate in both Irish and British coastal waters aggregate at the same time and location in the eastern Celtic Sea during the assumed peak spawning season.

6. Genetics information obtained from fish sampled as part of the studies reported in this thesis suggest that it is highly likely that sea bass from inshore Irish waters and from offshore waters in the Celtic Sea are part of the same panmictic population

As a consequence of this, the sustainable management and conservation of sea bass in Irish waters must be undertaken on a basis which is international, as well as local.

At an international level, the sustainable future of sea bass in Irish waters may be highly dependent on recruitment from the offshore spawning aggregations, such as those in the Celtic Sea. Management of this fishery, which extends across the jurisdictions of a number of countries and different ICES management divisions, may be crucial to ensuring the conservation of sea bass in Irish waters. While the current management of sea bass stocks in Irish waters may not be favourable to the Irish commercial fishing industry, there is no justification for a change in the status of the fishery within both inshore and offshore waters here, particularly when taking the general decline of sea bass stocks across Europe into consideration.

In an effort to conserve stocks of sea bass not only in Irish waters, but for all regions surrounding the Celtic Sea, serious consideration should be given to a regional management approach which considers the Celtic Sea stock as a single management unit, similar to the management plan of Atlantic cod stocks based on DST data suggested by Neat *et al.* (2014). A management committee comprised of the various stakeholders, including scientific, commercial and recreational concerns, from all nations operating within the regional fishery could be established to decide on optimal management plans. It could be recommended that a temporary sea bass spawning box, similar to that of the cod spawning box enforced through

Council Regulation (EC) No. 43/2009 (EC, 2009), be implemented in the Celtic Sea and other areas where aggregations of spawning sea bass are likely to occur to prevent targeted and accidental catches of sea bass during spawning.

At a national level, in Irish inshore waters the effects of fishing mortality from the recreational fishery on sea bass stocks are assumed to be relatively limited, with many anglers practising catch and release. However, as highlighted in the research of this thesis and documented by other telemetry studies on sea bass in Irish waters (Doyle *et al.*, 2017), there is still a threat posed to sea bass via illegal, unreported and unregulated (IUU) fishing activities within Irish inshore waters particularly when taking into account the restriction of the majority of sea bass movements in inshore waters to relatively discrete stretches of coastline, in addition to annual feeding site fidelity. It is therefore recommended that the conservation of stocks in inshore waters could be achieved through education of anglers regarding the benefits of ‘catch-and-release’ while also increasing patrols to limit IUU fishing activities. Degradation of sea bass nursery habitats (through pollution or other anthropogenic sources) may also pose a rise to conservation efforts, with the designation of protected status to such areas perhaps a useful method to protect the species at a vulnerable stage in its life cycle. Additionally, the effects of colder winter periods on the survival of juvenile sea bass can have a significant impact on recruitment to the fishery over time, so annual sampling of juvenile sea bass abundance and distribution in Irish nursery zones is highly recommended.

The efforts to conserve sea bass in Irish waters affects not only stocks here but also within Britain and France and possibly further afield. The success of these efforts depends on the willingness of national scientific and commercial interests to work in collaboration to realise the common goal of viable, mutually beneficial sea bass fishery within the Celtic Sea.

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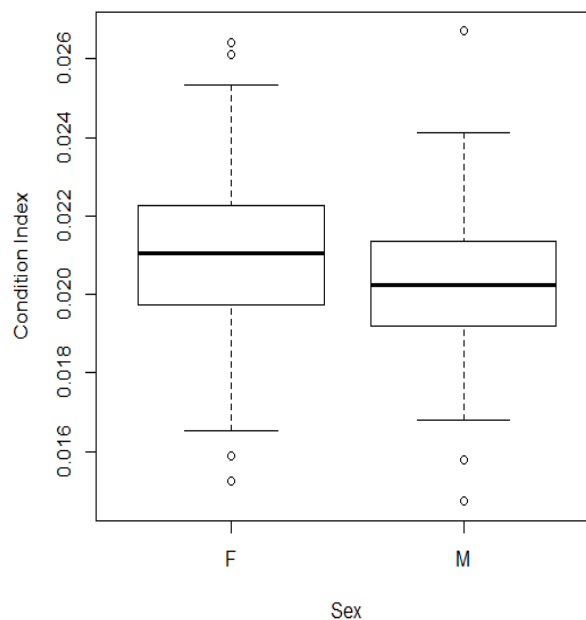
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Appendices

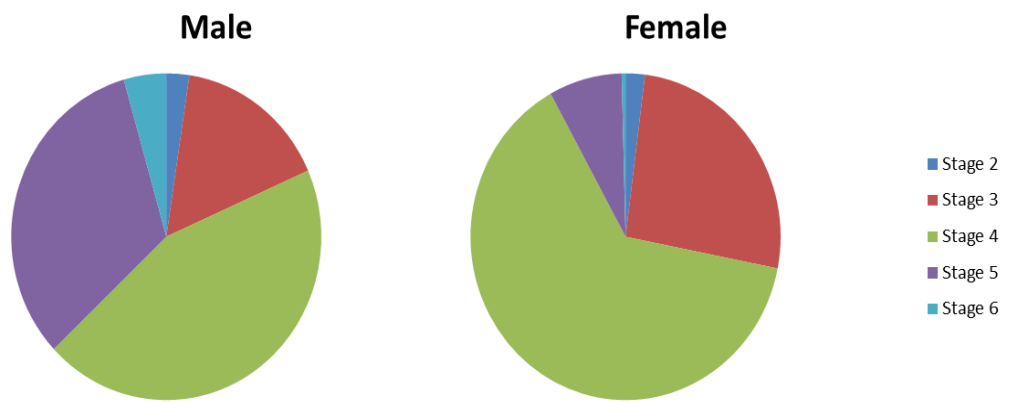
Appendix 1.0: Chapter 2

Appendix 1.1 Sexual maturity stages for European sea bass adopted from Pickett & Pawson (1994)

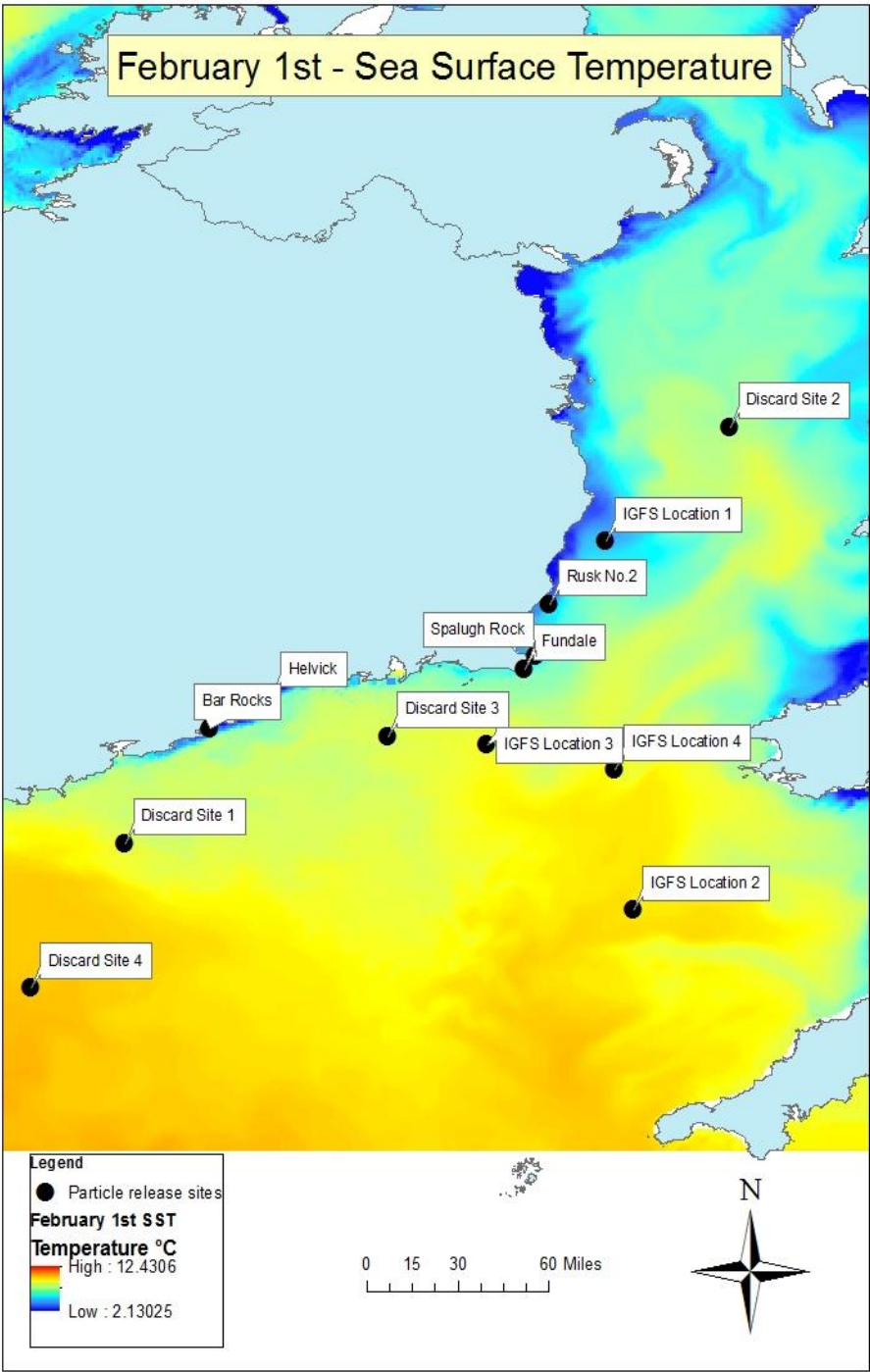
Stage Number	Male	Female
1 – Immature	Gonads ribbon-like; small; reddish-colourless	Gonads thin, reddish pink colour; threadlike
2 – Recovering/spent	Partly bloodshot in places; may be slightly opaque/grey in colour	Beginning to become opaque/pink; little vascularisation; no oocytes visible
3 – Early developing	Testes are off-white/grey in colour; thickness is 10-20% of their length	Oocytes begin to form; colour turns orange; becomes vascularised, translucent walls
4 – Late developing	White in colour; thickness less than 20% of length	Ovaries occupy 30-50% of ventral cavity; Oocytes visible by eye; orange-reddish colour
5 – Gravid/ripe	Sperm runs under pressure; bright white	Ovaries occupy >66% of ventral cavity; pale-yellow, orange; some haline eggs present; eggs run under pressure
6 – Running	Milt runs freely; grey-white in colour; very full	Haline eggs run freely; plump; vivid orange colour; transparent ovary wall
7 - Spent	Flattened; grey with tinges of red/pink	Flaccid; deep red; atretic eggs may be present



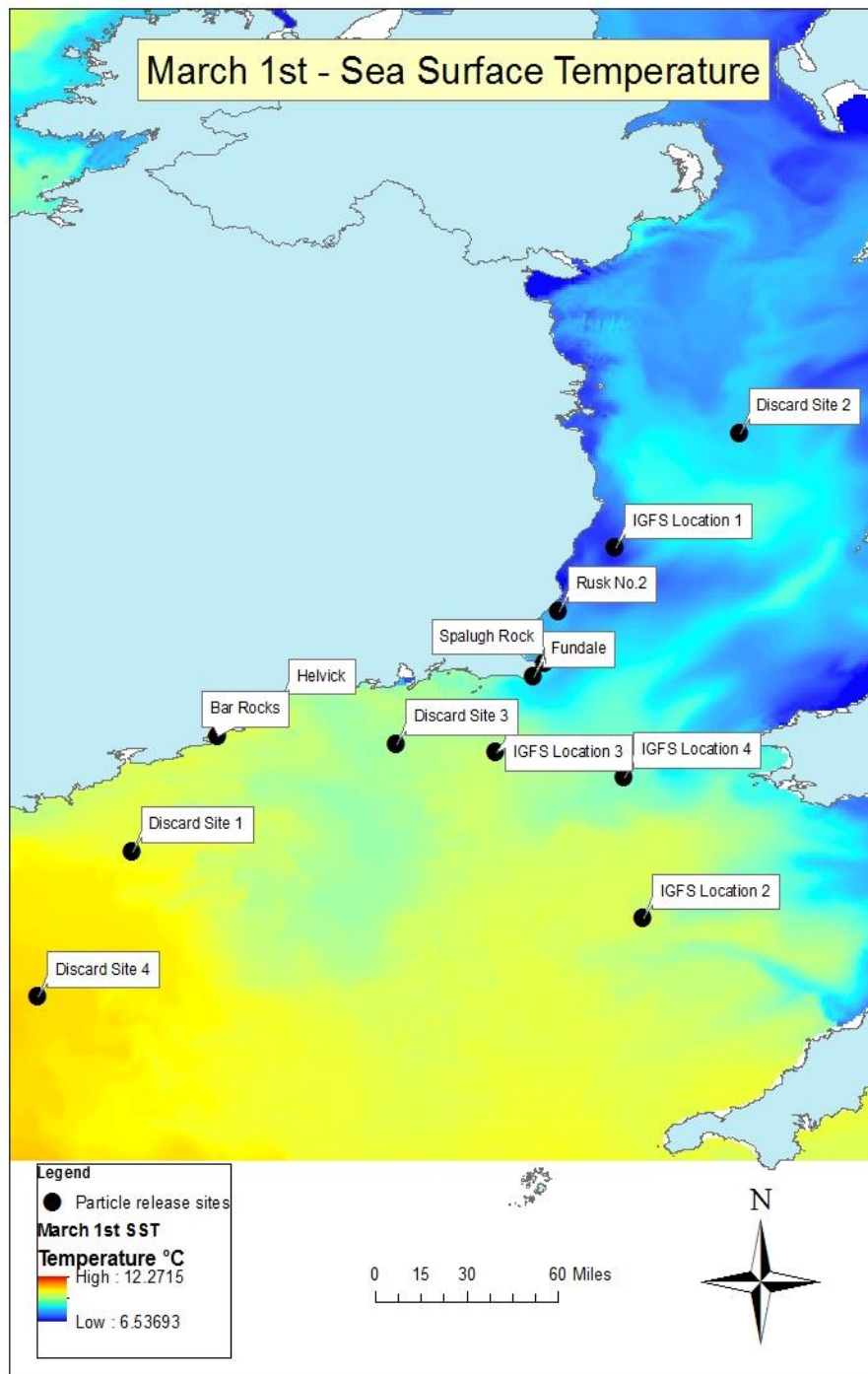
Appendix 1.2 Overall condition index for males (n = 294) and females (n = 248) for all fish from IGFS 2003 to 2015 where length/weight data was available



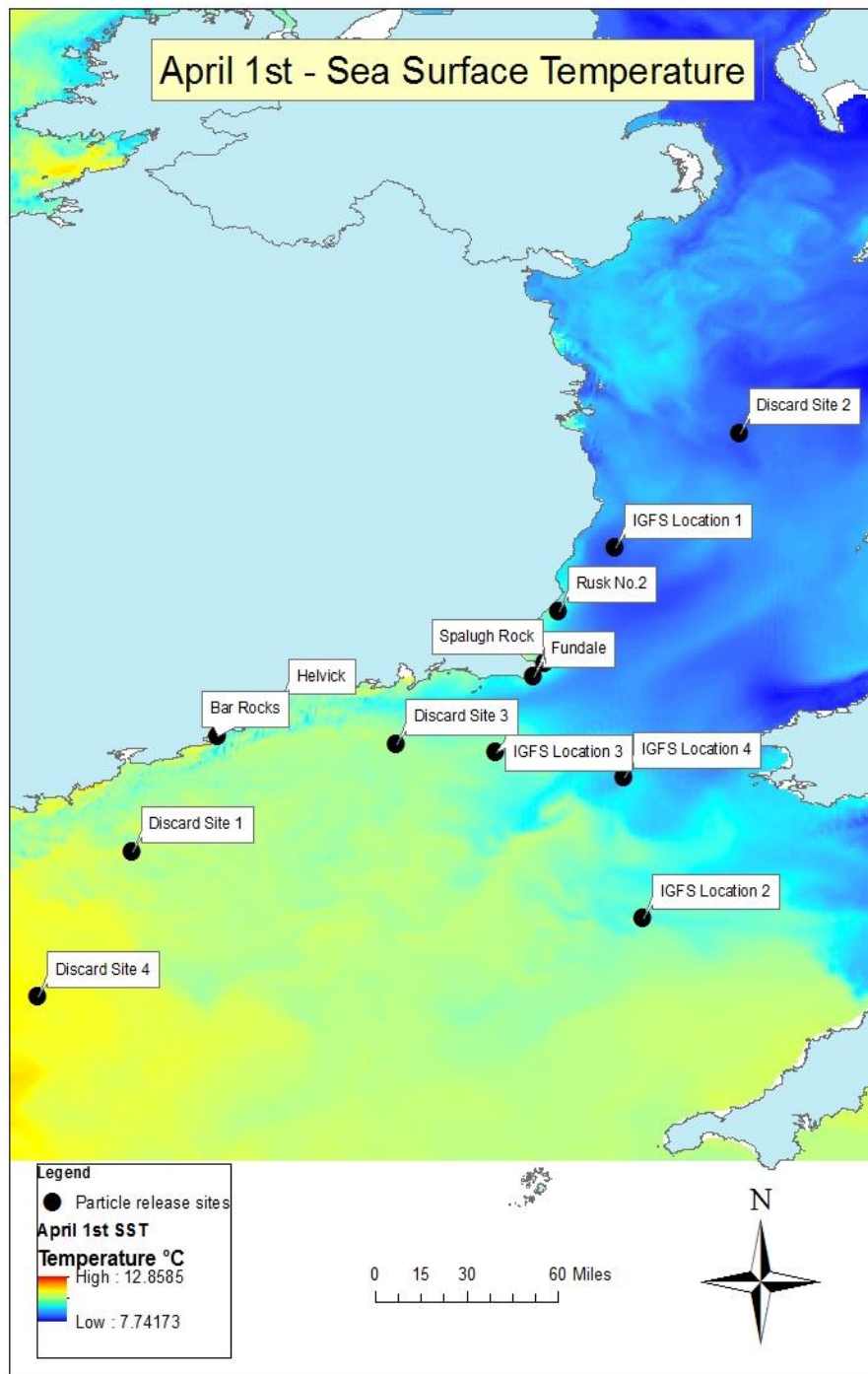
Appendix 1.3 Distribution of maturities between sexes (male = 294; female = 249) for all fish where data was available from 2008-2015



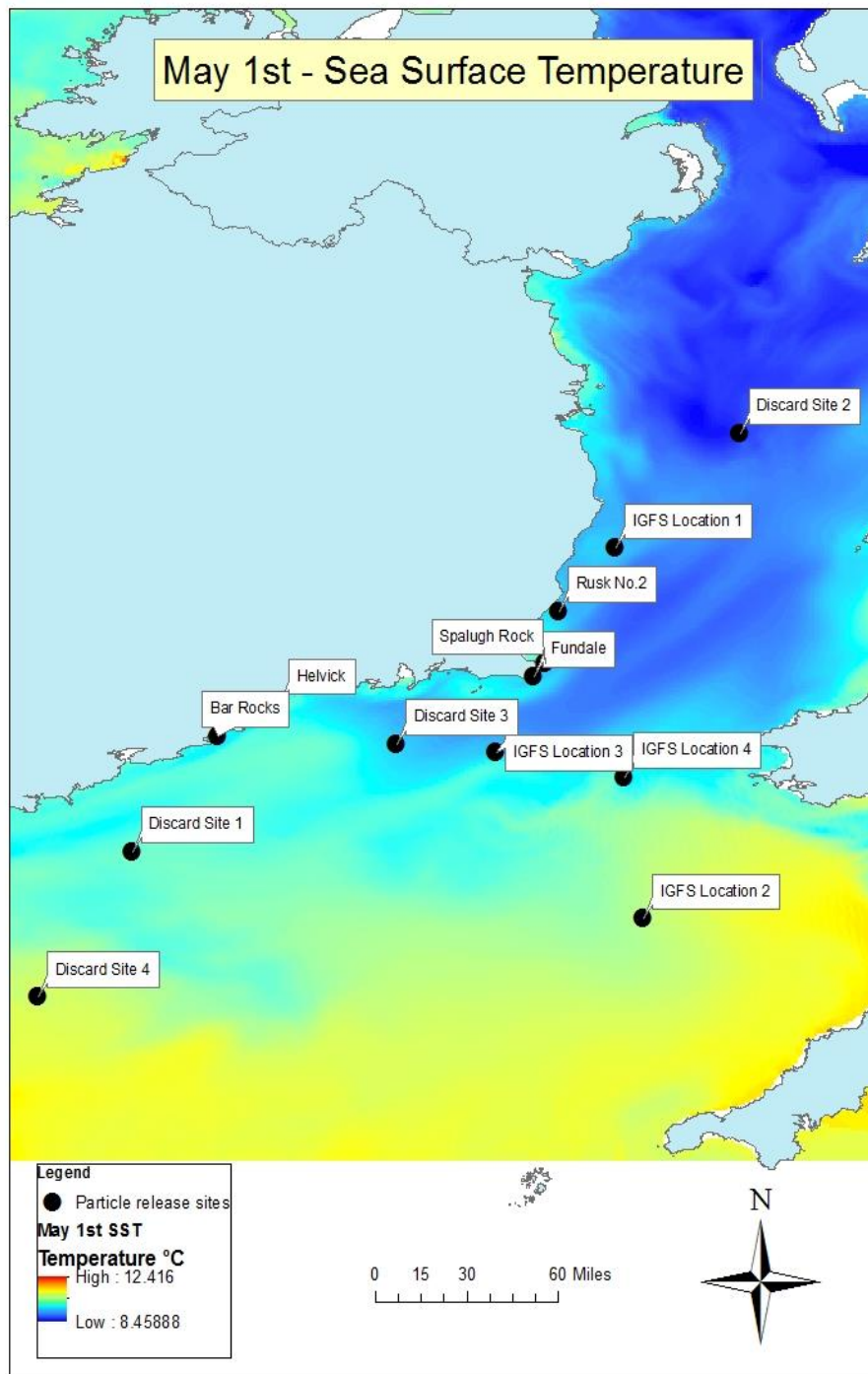
Appendix 2.1 Modelled sea surface temperature at putative particle release locations on February 1st, 2012 based on 2012 ROMS data



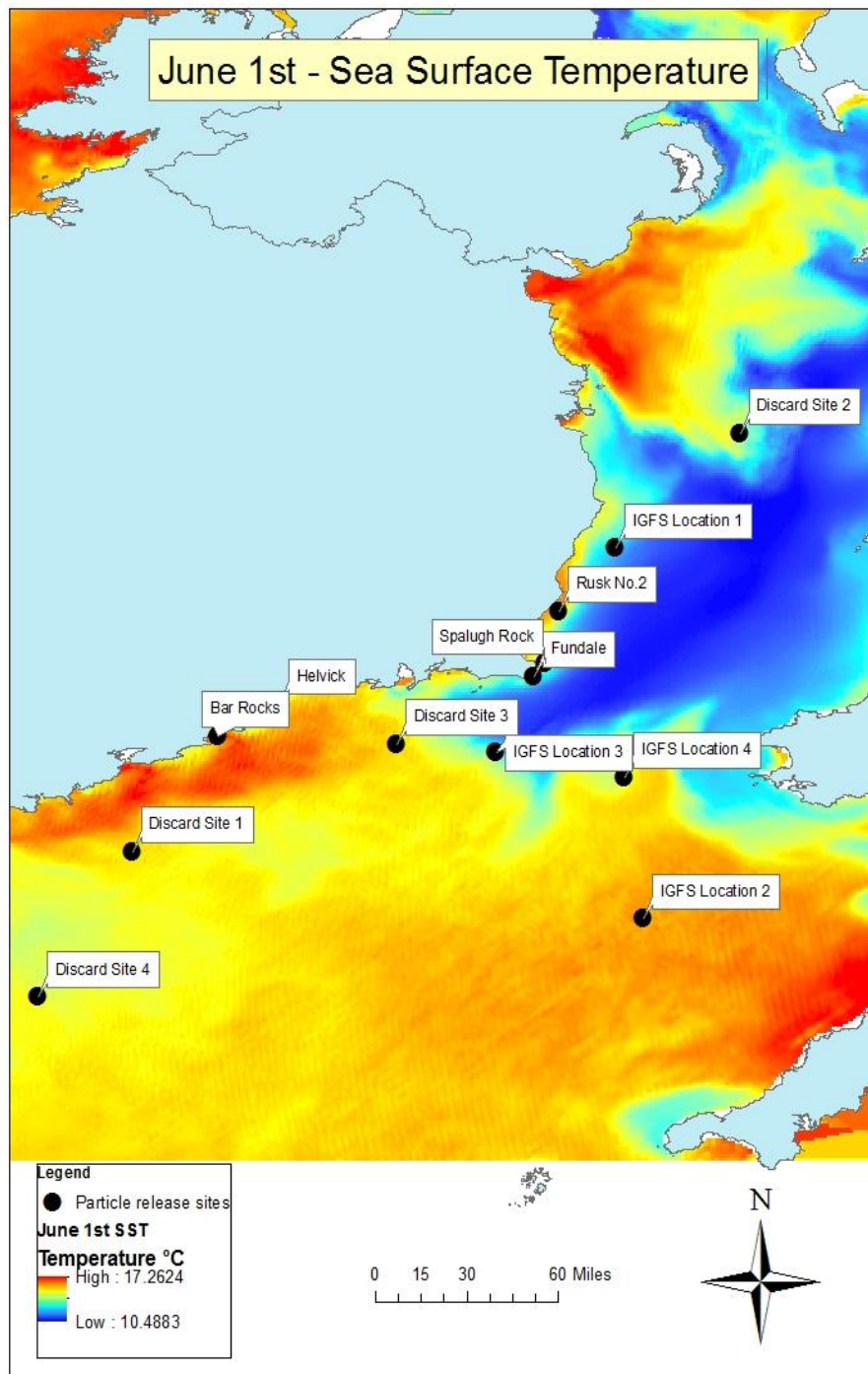
Appendix 2.2 Modelled sea surface temperature at putative particle release locations on March 1st, 2012 based on 2012 ROMS data



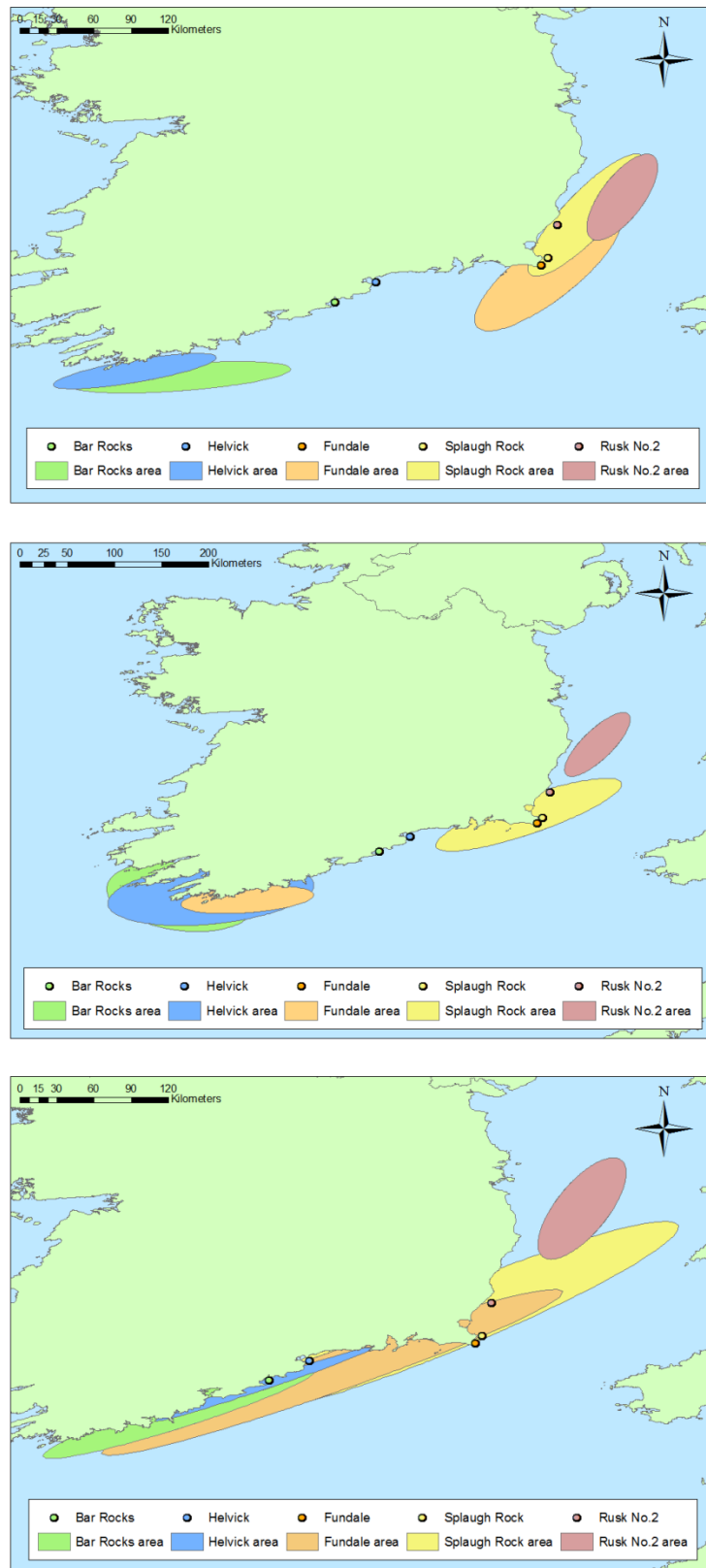
Appendix 2.3 Modelled sea surface temperature at putative particle release locations on April 1st, 2012 based on 2012 ROMS data



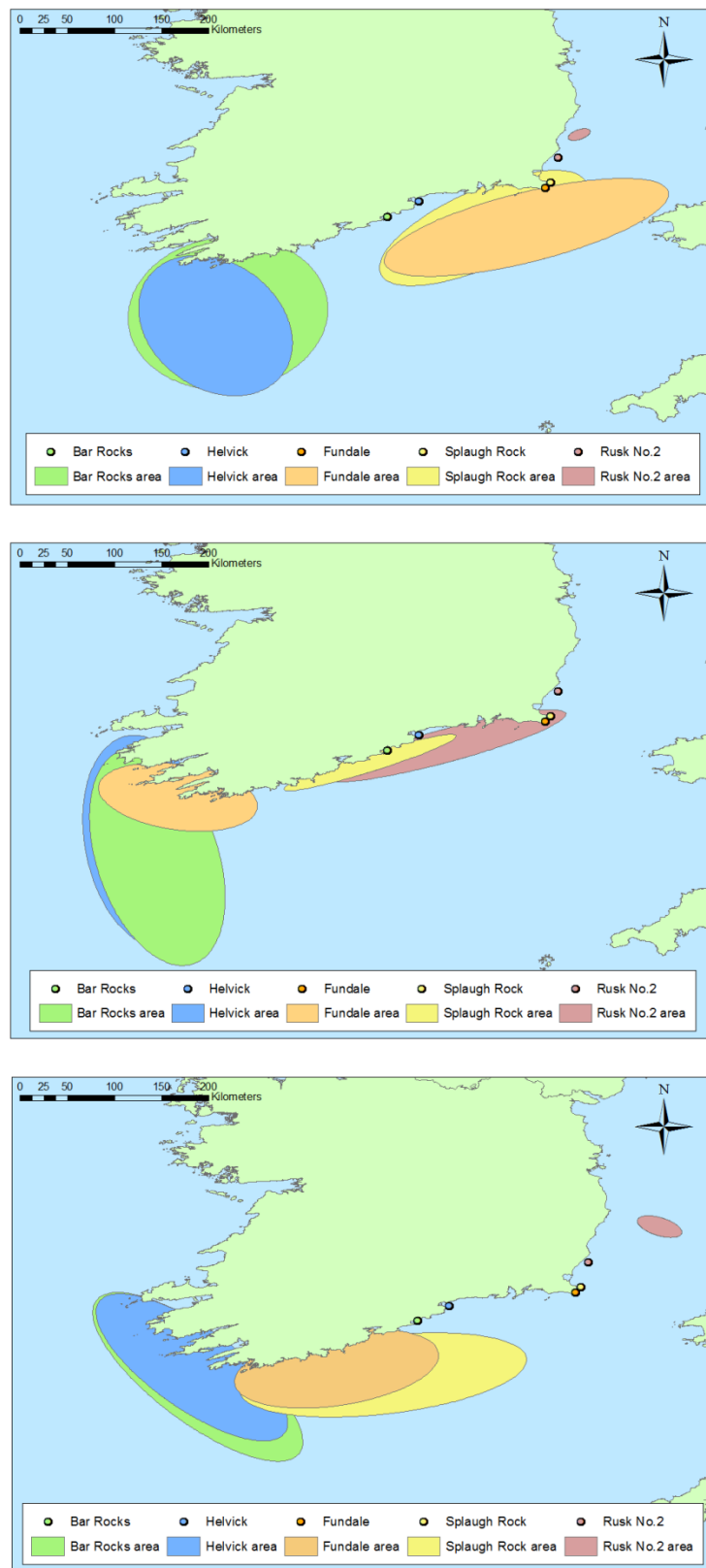
Appendix 2.4 Modelled sea surface temperature at putative particle release locations on May 1st, 2012 based on 2012 ROMS data



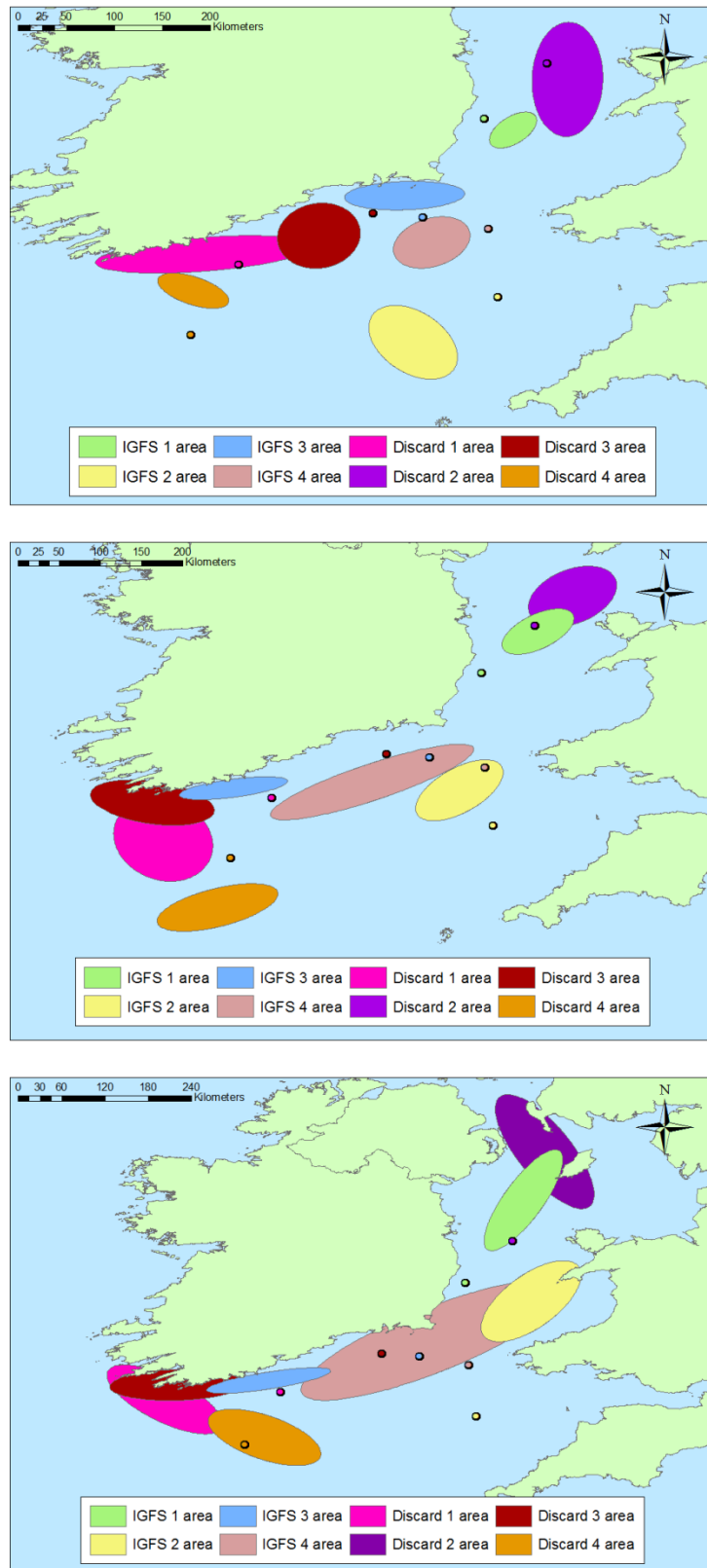
Appendix 2.5 Modelled sea surface temperature at putative particle release locations on February 1st, 2012 based on 2012 ROMS data



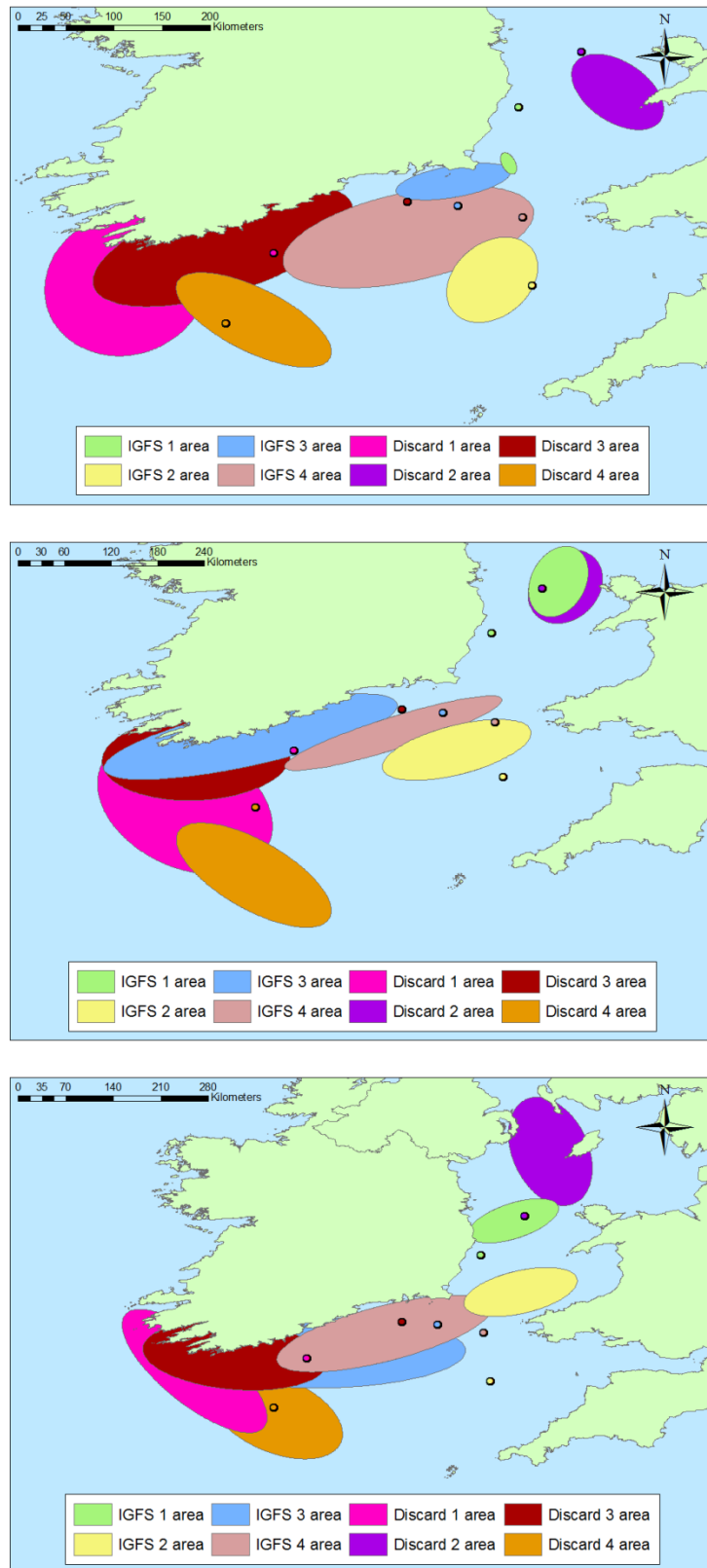
Appendix 2.6 DVM simulation output for March (top.), April (middle) and June (bottom) for inshore locations



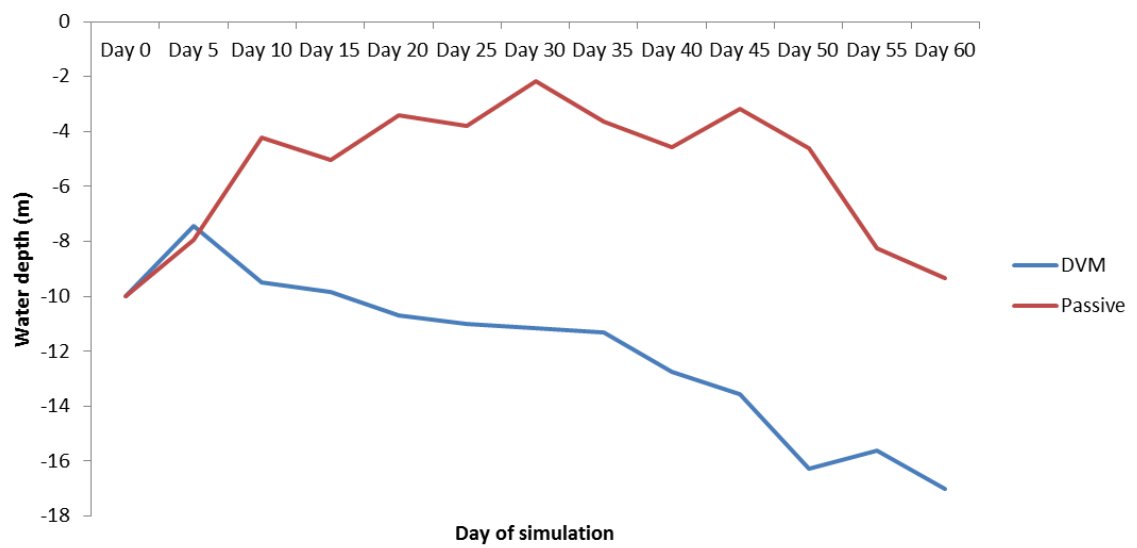
Appendix 2.7 Passive simulation output for March (top.), April (middle) and May (bottom)
for inshore locations



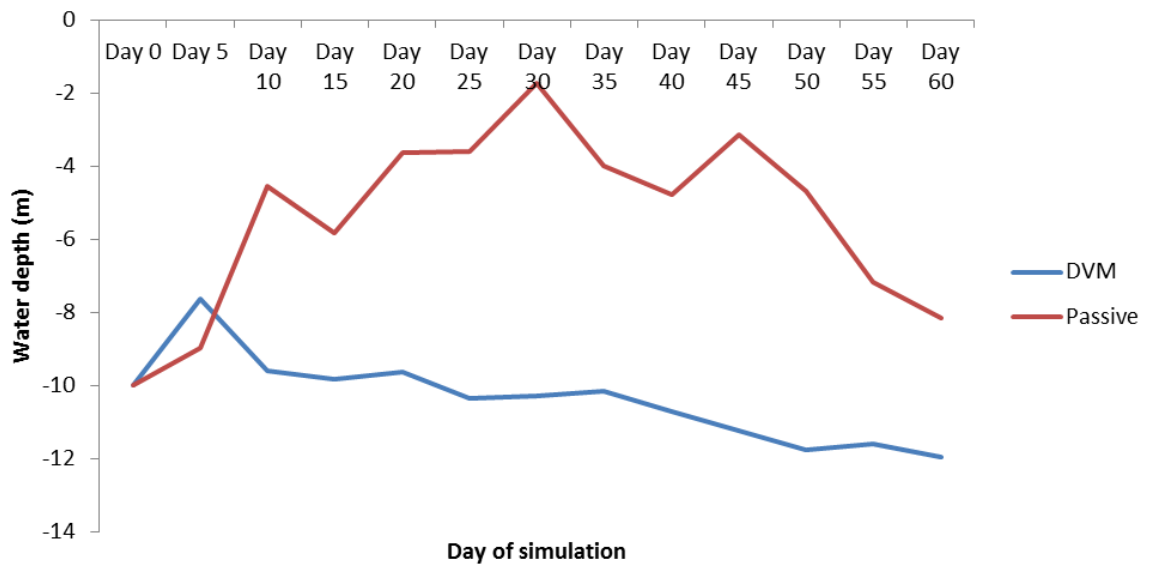
Appendix 2.8 DVM simulation output for February (top), April (middle) and May (bottom)
for offshore locations



Appendix 2.9 Passive simulation output for March (top), April (middle) and May (bottom)
for offshore locations



Appendix 2.10 Mean depth of particles from Bar Rocks June simulation at 5 day intervals



Appendix 2.11 Mean depth of particles from Helvick June simulation at 5 day intervals

Appendix 3.0: Report - Exploratory offshore sea bass larval survey

Introduction

European sea bass are believed to spawn at locations in the Celtic Sea during the assumed spawning period between February and June. An exploratory survey was undertaken in April 2016 by the Marine Institute to identify the presence of sea bass larvae at inshore locations close to the Irish coast and at offshore locations in the Celtic Sea.

Materials and methods

A total of 78 stations were sampled between April 24th and May 1st, 2016 (Fig. 1). Sampling was undertaken continually in all stages of the diurnal cycle with stations approximately every two hours on average. Larval sampling was conducted using a MultiNet (50cm x 50 cm aperture; mesh diameter = 300µm) which was towed at a speed of 2.0-2.5 knots. Sampling of the water column at offshore locations where there was sufficient depth was achieved through the use of a single oblique tow of ten minutes duration to 50m depth. Shallower depths found at inshore locations resulted in double oblique tows to a depth of 25 metres, where possible, within the ten minute timeframe. All samples were processed washed and were investigated for macroscopic evidence for larval sea bass presence once aboard. Each sample was then split once aboard with half the sample stored in ethanol and the remainder stored in 4% formalin solution buffered with sea water to allow for egg analysis.



Fig. 1 Locations of sampling stations in Irish inshore waters and in offshore waters in the Celtic Sea which were sampled using a MultiNet to identify the presence of sea bass eggs and larvae

Results and discussion

During the six day survey, no evidence of the presence of sea bass larvae or eggs was recorded at any of the stations sampled. While very few sea bass eggs and larvae have been recorded in the wild previously, the most plausible explanation for the absence of sea bass

eggs and larvae during this survey is sub-optimal water temperatures. Sea bass are believed to require a minimum water temperature of at least 8.5°C to facilitate spawning (Thompson & Harrop, 1987; Pickett & Pawson, 1994). For the majority of the duration of this survey, water temperatures remained predominately below this threshold, varying between 8.0°C and 8.4°C, which would have limited spawning activity and, therefore, egg and larval abundance within the water column.

It is suggested that future sea bass egg and larval surveys should be undertaken later in the spawning season, such as in late May or June, as the warmer water temperatures will result in increased spawning activity, resulting in a greater distribution and abundance of eggs and larvae at spawning locations. Targeted inshore egg and larval surveys are also suggested to identify the possibility of inshore spawning, identifiable through the development stage of the sea bass egg or larva when it is caught in inshore waters, and to investigate local areas of larval retention.

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Appendix 4.0: An investigation into population structure of European sea bass (*Dicentrarchus labrax*, L.) within Irish coastal waters and the north-east Celtic Sea

Introduction

The majority of previous genetic analysis of sea bass has been focused on comparisons between Mediterranean stocks and those of the north-east Atlantic Ocean. Previous assessments of the state of European sea bass stock by ICES considered the stock across all E.U. waters as a single entity but the results of tagging studies in addition to genetic analysis (Fritsch *et al.*, 2007) suggest that a separate stock of sea bass may be present off the southern coastline of Ireland as should therefore potentially be considered a separate populations/stock (ICES, 2015).

To investigate this potential existence of stock structure within sea bass populations within the Celtic Sea in this study, the genetic variation of pre-spawning adult sea bass taken from an offshore aggregation in the north-east Celtic Sea was analysed (see Chapter 2). To further try and establish a link between offshore aggregations and inshore populations within Irish coastal waters, these results were compared with genetic analysis of fish captured from estuaries, beaches and other areas along the southern Irish coastline. The results were also compared these samples with sea bass caught in the North Sea to investigate potential genetic differences between sea bass stocks separated by geographic distance in the waters of north-west Europe.

Materials and methods

Sample acquisition

A total of 100 genetic samples were obtained for this study. Samples were in the form of tail clippings, taken from the upper section of the tail fin. Samples were stored in individually labelled vials in molecular-grade ethanol to preserve them. Of the 100 samples acquired, 50 samples were taken from fish in inshore Irish waters between June 2015 and April 2016. These fish were caught through a combination of angling and beach seine netting. Offshore samples were taken from fish which were caught in the north-east Celtic Sea onboard the *MRV Celtic Explorer* the *MRV Celtic Voyager* during research surveys (Fig. 1). Samples for sea bass from the North Sea (n=30) were provided by CEFAS in the form of dried scales stored in molecular-grade ethanol.

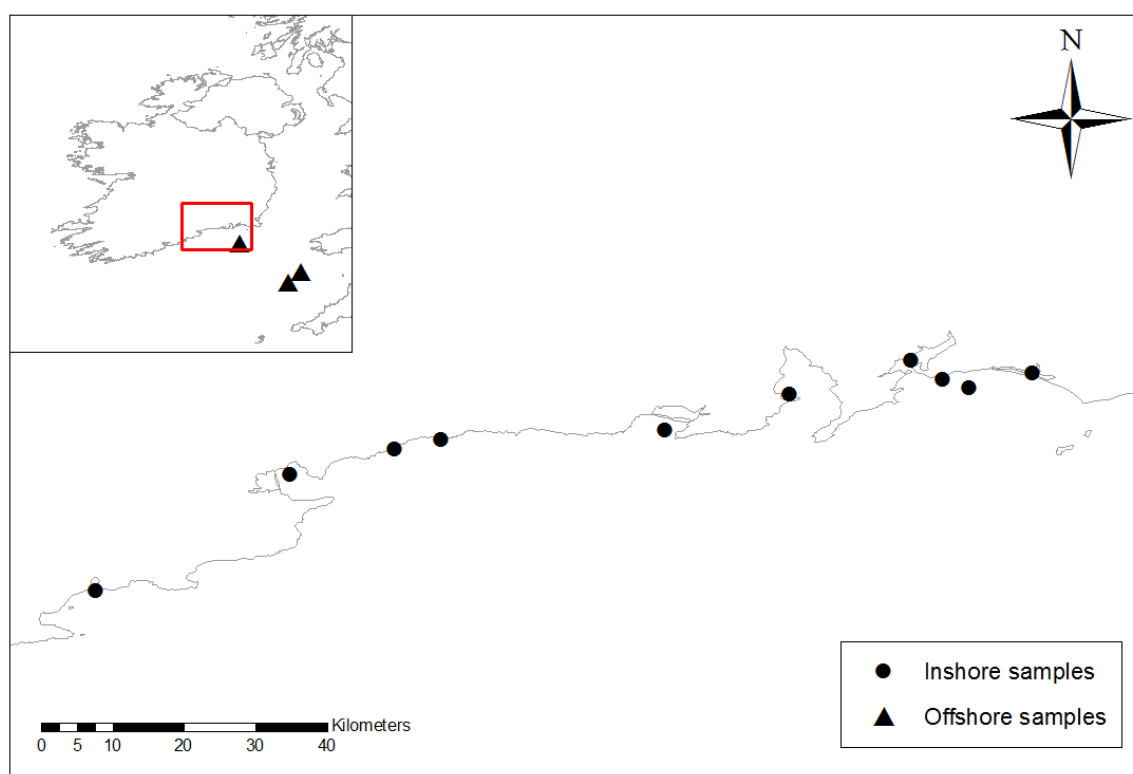


Fig. 1 Locations where inshore and offshore samples were taken in the Celtic Sea and on the Irish coast

Disclaimer: All genetic analysis and screening was undertaken by Paulo Prodl of Queens University Belfast (QUB), who is the author of the remainder of this *Materials and Methods* section and *Results* section.

Sample preparation

Genomic DNA was extracted using the Promega Wizard SV 96 genomic DNA purification system and transferred into 96 well microtitre plates for storage at -20°C prior to genetic analysis.

Genetic analysis

All samples were screened for a marker panel consisting of 14 sea bass (*Dicentrarchus labrax*) microsatellite loci developed by Chistiakov *et al.* (2005): DLA0012, DLA0013, DLA0014, DLA0018, DLA0019, DLA0109, DLA0110, DLA0113, DLA0119, DLA0015, DLA0020, DLA0104, DLA0105, DLA0116. Genetic screening was carried out on a 96 capillary ABI 3730XL DNA analyser following optimisation protocols routinely used by the Beaufort Fish Genetics Group at QUB. In brief, PCR were carried out in 3.5µl volumes on 96 well microtitre plates, consisting 1µl template DNA (~2-5 ng/µl), 1.75µl of PPP Top-Bio mastermix (Top-Bio) and 0.75 µl of a cocktail of ABI fluorescent labelled forward and/or unlabelled reverse 'pig' tailed PCR primers. PCR thermocycling conditions consisted of an initial denaturation step of 15 min at 95°C, followed by 28 cycles of 30 seconds at 94°C, 90 seconds at 57°C and 60 seconds at 72°C. This was followed by a final extension step of 30 min at 60°C. All reactions were carried out using Techne TC-Plus thermal cyclers, with a heated lid at 105°C.

Following PCR, amplicons were diluted 1:4 with ddH₂O and 1 µl transferred to a new 96 microtitre plate. To this, 9 µl of Hi-Di formamide/size standard mix (5 µl of GS Liz 600 size standard added to 900 µl of Hi-Di formamide, both chemicals from Applied Biosystems) was added to each well. Diluted PCR products were run on a 96 capillary ABI 3730XL DNA analyser, and the fragment size analysis (i.e. allelic calls) for genotypes was carried out using GENEMAPPERv4.1 (Applied Biosystems, TM). Genotypes for each microsatellite locus/specimen were individually checked and manually confirmed prior to their addition to an electronic Excel based genotypic database. Over 70% of the genotyping was independently scored to ensure consistent scoring and to minimise scoring errors.

Data analysis

Summary population sample statistics, including estimates of allelic frequencies, observed (H_o) and expected (H_e) heterozygosities, number of alleles (N_a) per locus, allele richness, were calculated using the *divBasic* function as implemented in *diveRsity* v1.9.89 (Keenan *et al.*, 2013). Tests for departure from Hardy-Weinberg Expectations (HWE) were carried out using GENEPOPv4.3 (Rousset, 2008). To test for genetic differentiation among population samples (i.e. testing for population sub-structuring), three approaches were employed.

The first involved the use of Weir & Cockerham's (1984) equivalent (θ) of Wright's F -statistics. More recently, Jost (2008) discussed potential biases that affect standard F_{ST} statistics when estimated from highly polymorphic microsatellite markers, and proposed alternative related statistics to account for this bias in order to accurately reflect levels of population genetic structuring. To allow for this bias, the more recently derived related standardized statistics D_{Jost} (Jost, 2008) was estimated using *diveRsity* v1.9.89 (Keenan, *et al.*, 2013). The second analysis involved the Bayesian analytical framework proposed by Pritchard *et al.* (2000) and implemented in the programme STRUCTURE V2.3. Given a set

of samples (irrespective of origin or initial hypothesis), the STRUCTURE Bayesian algorithm assess the best number of distinct genetic entities (populations) explaining the samples. STRUCTURE runs were repeated 20 times for each K value (i.e. number of genetic groups being tested), which ranged from 1 to 10 with the following parameters: Length of Burn-in Period = 100,000; Number of MCMC Reps after Burning = 100,000; Admixture model, Allele Frequencies Correlated. Summary results from multiple STRUCTURE runs (i.e. iterations) for best K value were collated using CLUMPP (Jakobsson & Rosenberg, 2007) with the following parameters: Greedy search method with option 2 for random input orders set to 20,000. Third, the discriminant analysis of principal components (dapc) analytical framework proposed by Jombart *et al.* (2010) was also employed to confirm/verify results. Similar to STRUCTURE, this non-parametric multivariate method allows for the identification of groups of more genetically related individuals (i.e. “populations”) within data set comprising of individual genotypes. The approach also provides a useful graphical assessment of between/among population genetic differences (i.e. principal components plot).

Results

Microsatellite multilocus genotypes were successfully obtained for 93 individuals (71% of processed samples). Average success amplification success varied among samples as follows: Inshore (84%), Offshore (52%), North Sea (80%). Within sample sets, some variation was also observed in terms of success amplification per locus. In all instances, *DLA0013* was the most problematic (i.e. failed amplifications despite repetitive attempts). Close examination of this locus, indicate the existence of a high incidence of “null alleles”, thus the non-amplification most likely related to “null” homozygotes. This marker locus was excluded from subsequent population analysis. Two additional loci (*DLA0012* and *DLA0110*) consistently failed to amplify for all samples screened and were also removed from

subsequent analysis. Summary sample statistics for the remaining marker loci (including *DLA0013*) are displayed in Fig. 1 and Tables 1 and 2. Average allelic richness was similar ($ar = 11$ for both Inshore and Offshore samples and $ar = 10$ for North Sea) and all samples displayed very similar levels of heterozygosity (ca 70%). With one exception (*DLA0013* – explained by the presence of “null” alleles), there was no evidence for departures from HWE expectations. In general, all samples shared same alleles at very similar frequencies. Unique alleles were present at very low frequencies and, hence, are most likely an artefact of limited sampling sizes.

Pair-wise F_{st} estimators of population sample divergence are displayed in Figure 2 and Table 3. Both standard (θ) and unbiased corrected estimators (D_{jost}) are presented. The standard estimator is presented to allow for a direct comparison with results reported in the previous studies in the literature.

In the current study, uncorrected pair-wise F_{st} values ranged from 0.0006 (corrected $D_{jost} = 0.004$) between Inshore and North Sea to 0.0028 between Offshore and North Sea (corrected $D_{jost} = 0.0054$). All three pair-wise comparisons were found to be statistically non-significant implying that there is no evidence suggesting that the samples belong to distinct populations. The result of the *STRUCTURE* analysis, summarised in Fig. 3, confirm the absence of noticeable population sub-structuring among samples. The only interesting observation is linked to two particular individuals that appear do belong to a distinct genetic cluster. While this is an interesting observation, sample sizes are too small to allow for any meaningful biological interpretation. Similarly to the two previous analyses, the results of dapc approach again confirm the lack of genetic sub-structuring among samples (Fig. 4).

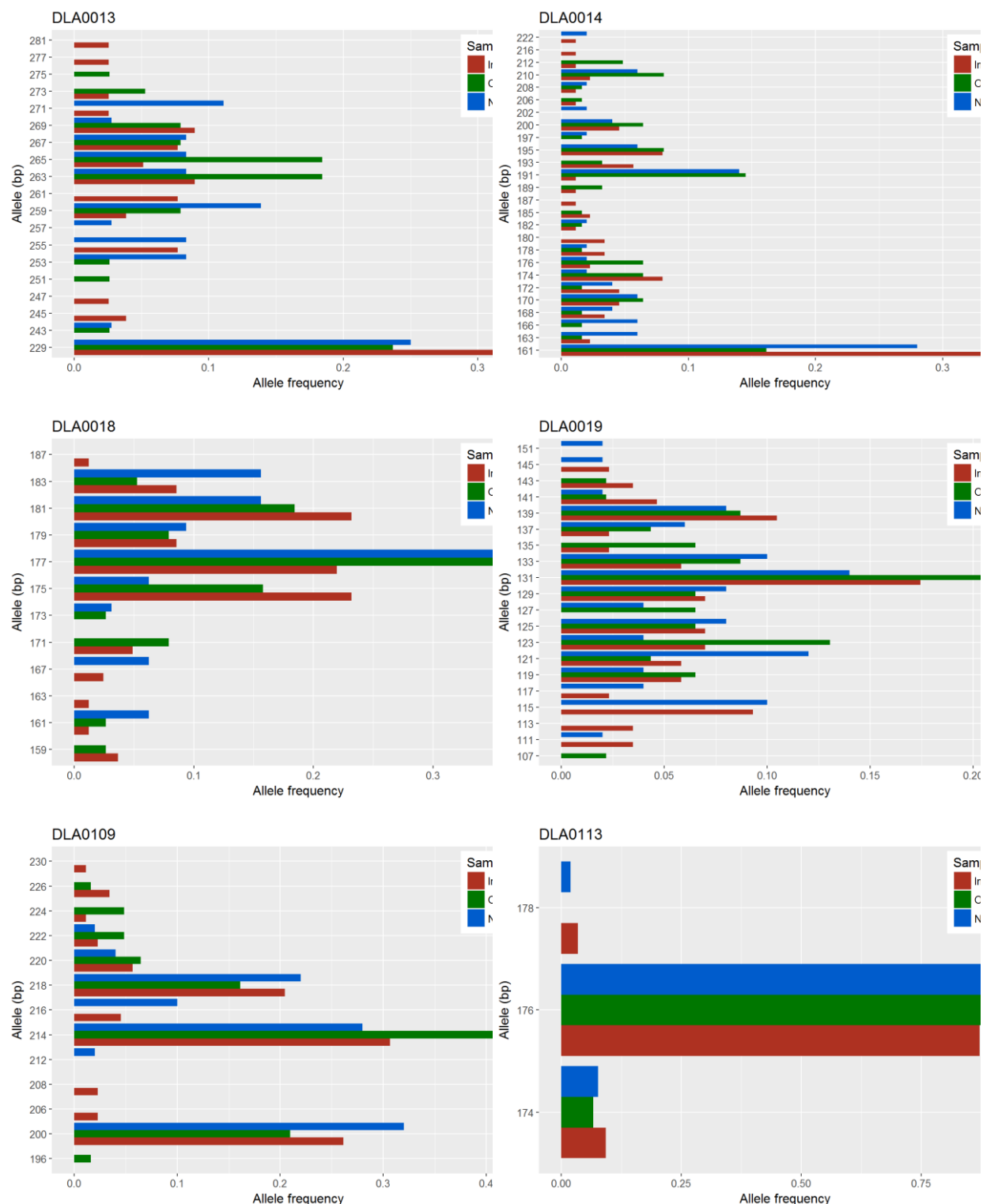


Fig. 1 Allele frequency distribution for 12 sea bass (*Dicentrarchus labrax*) microsatellite marker loci.

Fig. 1 Continuation

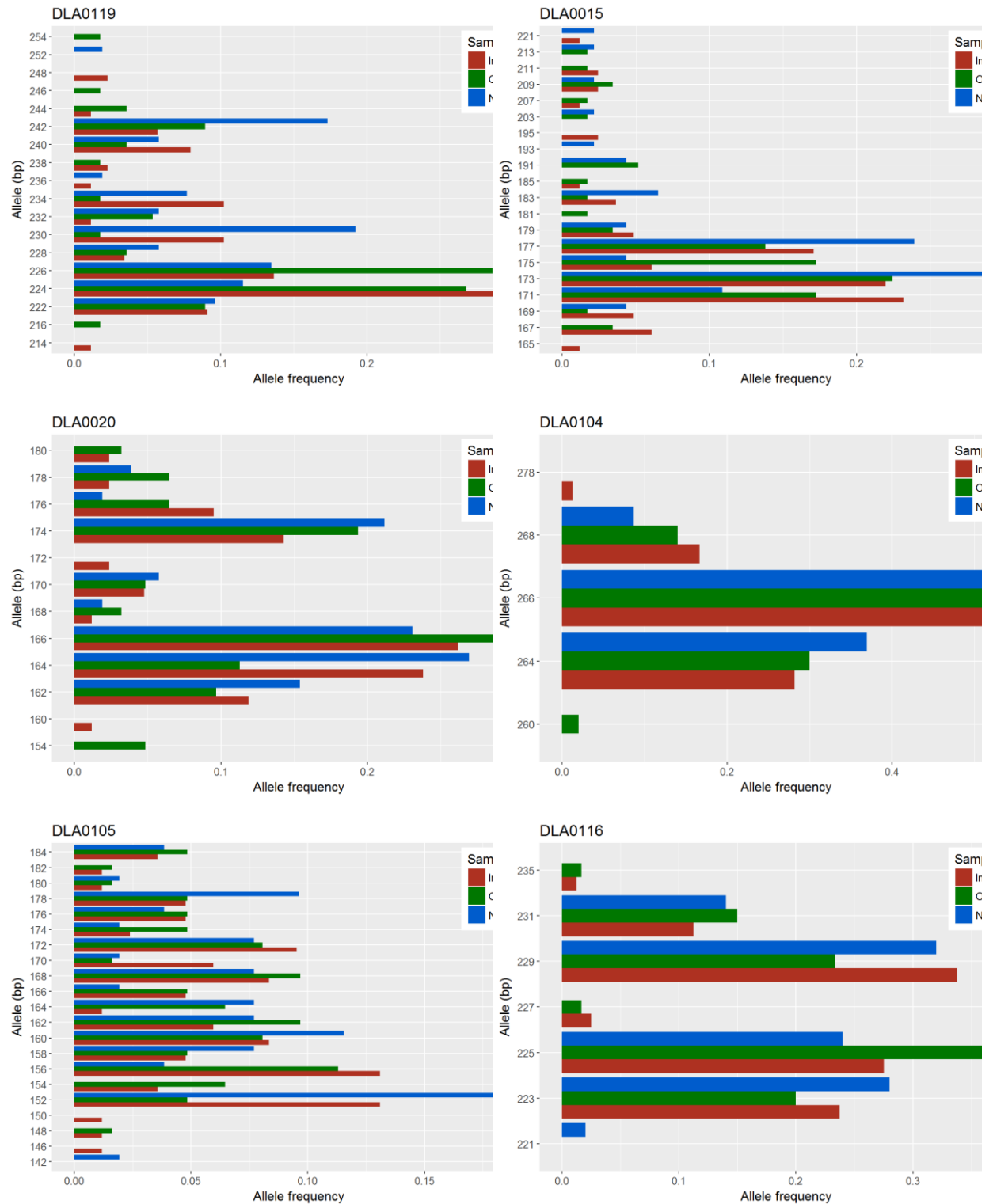


Table 1. Summary population sample statistics including allele richness (ar), number of successfully amplified (PCR) samples (N), observed and expected heterogositities (Obs and Exp Het) and test for conformance to Hardy Weinberg Equilibrium (HWE – ‘ns’ non-significant)

Inshore													
Locus	DLA0013	DLA0014	DLA0018	DLA0019	DLA0109	DLA0113	DLA0119	DLA0015	DLA0020	DLA0104	DLA0105	DLA0116	overall
ar	12.1	18.0	8.4	15.7	9.5	2.9	12.0	12.5	9.8	3.6	17.4	5.5	11
N	39	44	41	43	44	43	44	41	42	39	42	40	42
Obs Het	0.487	0.909	0.805	0.953	0.750	0.233	0.864	0.854	0.881	0.436	0.952	0.750	0.739
Exp Het	0.846	0.847	0.825	0.917	0.787	0.230	0.846	0.853	0.827	0.603	0.923	0.741	0.770
HWE	P<0.001	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Offshore													
Locus	DLA0013	DLA0014	DLA0018	DLA0019	DLA0109	DLA0113	DLA0119	DLA0015	DLA0020	DLA0104	DLA0105	DLA0116	overall
ar	10.8	19.0	8.5	14.0	7.6	2.0	13.6	14.2	9.9	3.9	17.3	5.7	11
N	19	31	19	23	31	30	28	29	31	25	31	30	27
Obs Het	0.368	0.871	0.947	0.870	0.742	0.133	0.821	0.931	0.839	0.400	1.000	0.533	0.705
Exp Het	0.852	0.916	0.788	0.894	0.731	0.124	0.822	0.863	0.831	0.598	0.930	0.736	0.757
HWE	P<0.001	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
North Sea													
Locus	DLA0013	DLA0014	DLA0018	DLA0019	DLA0109	DLA0113	DLA0119	DLA0015	DLA0020	DLA0104	DLA0105	DLA0116	overall
ar	11.0	18.0	8.0	15.7	7.0	3.0	11.0	13.0	8.0	3.0	16.0	5.0	10
N	18	25	16	25	25	26	26	23	26	23	26	25	24
Obs Het	0.444	0.960	0.750	0.840	0.680	0.192	0.885	0.783	0.923	0.348	0.885	0.880	0.714
Exp Het	0.869	0.876	0.789	0.915	0.758	0.177	0.876	0.824	0.800	0.560	0.905	0.742	0.758
HWE	P<0.001	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table. 2 Allele Frequency distribution for 12 European sea bass (*Dicentrarchus labrax*) microsatellite marker loci

DLA0013				DLA0014				DLA0018			
alleles	Inshore	Offshore	North Sea	alleles	Inshore	Offshore	North Sea	alleles	Inshore	Offshore	North Sea
229	0.333	0.237	0.250	161	0.352	0.161	0.280	159	0.037	0.026	-
243	-	0.026	0.028	163	0.023	0.016	0.060	161	0.012	0.026	0.063
245	0.038	-	-	166	-	0.016	0.060	163	0.012	-	-
247	0.026	-	-	168	0.034	0.016	0.040	167	0.024	-	0.063
251	-	0.026	-	170	0.045	0.065	0.060	171	0.049	0.079	-
253	-	0.026	0.083	172	0.045	0.016	0.040	173	-	0.026	0.031
255	0.077	-	0.083	174	0.080	0.065	0.020	175	0.232	0.158	0.063
257	-	-	0.028	176	0.023	0.065	0.020	177	0.220	0.368	0.375
259	0.038	0.079	0.139	178	0.034	0.016	0.020	179	0.085	0.079	0.094
261	0.077	-	-	180	0.034	-	-	181	0.232	0.184	0.156
263	0.090	0.184	0.083	182	0.011	0.016	0.020	183	0.085	0.053	0.156
265	0.051	0.184	0.083	185	0.023	0.016	-	187	0.012	-	-
267	0.077	0.079	0.083	187	0.011	-	-				
269	0.090	0.079	0.028	189	0.011	0.032	-				
271	0.026	-	0.111	191	0.011	0.145	0.140				
273	0.026	0.053	-	193	0.057	0.032	-				
275	-	0.026	-	195	0.080	0.081	0.060				
277	0.026	-	-	197	-	0.016	0.020				
281	0.026	-	-	200	0.045	0.065	0.040				
				202	-	-	0.020				
				206	0.011	0.016	-				
				208	0.011	0.016	0.020				
				210	0.023	0.081	0.060				
				212	0.011	0.048	-				
				216	0.011	-	-				
				222	0.011	-	0.020				

DLA0019				DLA0109				DLA0113			
alleles	Inshore	Offshore	North Sea	alleles	Inshore	Offshore	North Sea	alleles	Inshore	Offshore	North Sea
107	-	0.022	-	196	-	0.016	-	174	0.093	0.067	0.077
111	0.035	-	0.020	200	0.261	0.210	0.320	176	0.872	0.933	0.904
113	0.035	-	-	206	0.023	-	-	178	0.035	-	0.019
115	0.093	-	0.100	208	0.023	-	-				
117	0.023	-	0.040	212	-	-	0.020				
119	0.058	0.065	0.040	214	0.307	0.435	0.280				
121	0.058	0.043	0.120	216	0.045	-	0.100				
123	0.070	0.130	0.040	218	0.205	0.161	0.220				
125	0.070	0.065	0.080	220	0.057	0.065	0.040				
127	-	0.065	0.040	222	0.023	0.048	0.020				
129	0.070	0.065	0.080	224	0.011	0.048	-				
131	0.174	0.217	0.140	226	0.034	0.016	-				
133	0.058	0.087	0.100	230	0.011	-	-				
135	0.023	0.065	-								
137	0.023	0.043	0.060								
139	0.105	0.087	0.080								
141	0.047	0.022	0.020								
143	0.035	0.022	-								
145	0.023	-	0.020								
151	-	-	0.020								

Table. 2 Continuation

DLA0119				DLA0015				DLA0020			
alleles	Inshore	Offshore	North Sea	alleles	Inshore	Offshore	North Sea	alleles	Inshore	Offshore	North Sea
214	0.011	-	-	165	0.012	-	-	154	-	0.048	-
216	-	0.018	-	167	0.061	0.034	-	160	0.012	-	-
222	0.091	0.089	0.096	169	0.049	0.017	0.043	162	0.119	0.097	0.154
224	0.307	0.268	0.115	171	0.232	0.172	0.109	164	0.238	0.113	0.269
226	0.136	0.286	0.135	173	0.220	0.224	0.304	166	0.262	0.306	0.231
228	0.034	0.036	0.058	175	0.061	0.172	0.043	168	0.012	0.032	0.019
230	0.102	0.018	0.192	177	0.171	0.138	0.239	170	0.048	0.048	0.058
232	0.011	0.054	0.058	179	0.049	0.034	0.043	172	0.024	-	-
234	0.102	0.018	0.077	181	-	0.017	-	174	0.143	0.194	0.212
236	0.011	-	0.019	183	0.037	0.017	0.065	176	0.095	0.065	0.019
238	0.023	0.018	-	185	0.012	0.017	-	178	0.024	0.065	0.038
240	0.080	0.036	0.058	191	-	0.052	0.043	180	0.024	0.032	-
242	0.057	0.089	0.173	193	-	-	0.022				
244	0.011	0.036	-	195	0.024	-	-				
246	-	0.018	-	203	-	0.017	0.022				
248	0.023	-	-	207	0.012	0.017	-				
252	-	-	0.019	209	0.024	0.034	0.022				
254	-	0.018	-	211	0.024	0.017	-				
				213	-	0.017	0.022				
				221	0.012	-	0.022				

Fig. 2 Pair-wise F -statistics comparisons [both Weir & Cockerham (1984) θ and Jost (2008) D_{Jost}] among population samples surveyed. ‘Red’ dot represent actual F_{st} estimate in each pairwise comparison. The ‘blue’ error bars represent the 95% confidence intervals for the estimates. The “green” dashed line represent the theoretical expected value ($F_{st}=0$) of the estimates assuming panmixia (i.e. no population substructuring).

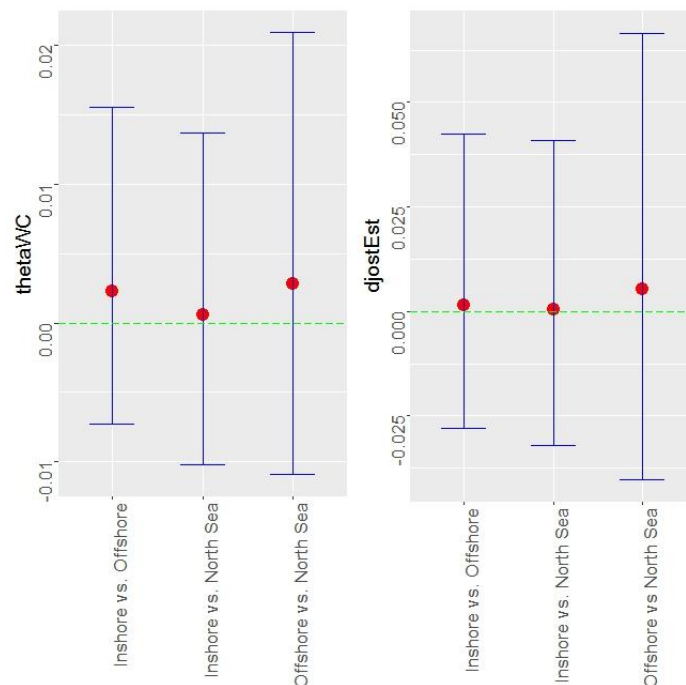


Table 3. Pair-wise F -statistics comparisons A) Weir & Cockerham (1984) θ and B) Jost (2008) D_{Jost} among population samples surveyed. F_{st} estimates between population samples are displayed below diagonal in each case. Values in parenthesis above diagonal represent the 95% confidence intervals (C.I.) for the estimates. In all instances, the 95% C.I. overlap the expected theoretical value ($F_{st}=0$) of the estimates assuming panmixia (i.e. no population sub-structuring).

A)	Inshore	Offshore	North Sea
Inshore	-	(-0.0073 - 0.0155)	(-0.0102 - 0.0137)
Offshore	0.0023	-	(-0.0109 - 0.0209)
North Sea	0.0006	0.0028	-

B)	Inshore	Offshore	North Sea
Inshore	-	(-0.028 - 0.042)	(-0.032 - 0.041)
Offshore	0.0015	-	(-0.041 - 0.066)
North Sea	0.0004	0.0054	-

Fig. 3 Summary bar plot for STRUCTURE analysis: while samples are best explained by two main genetic clusters (red and blue), the blue group is anchored by two individuals only. All remaining samples seem to belong to the red group.

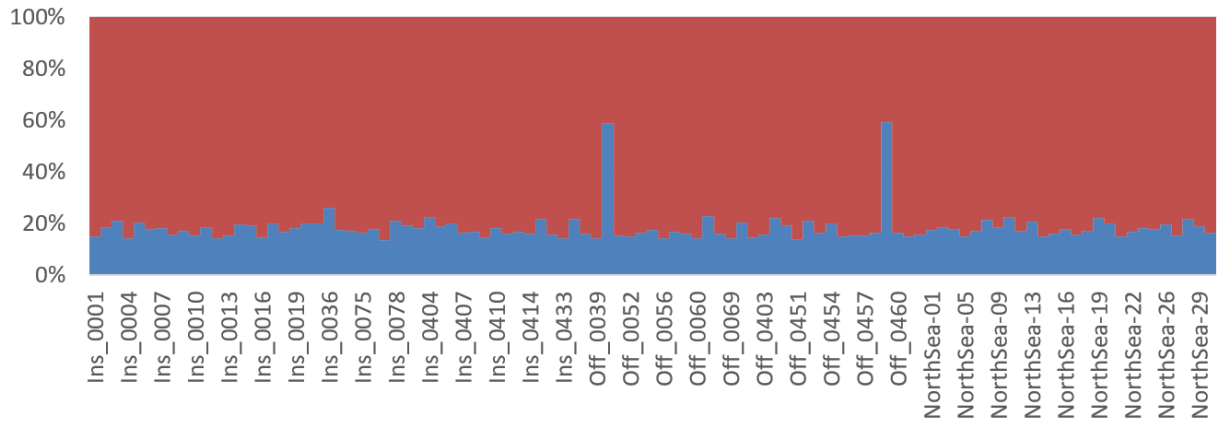
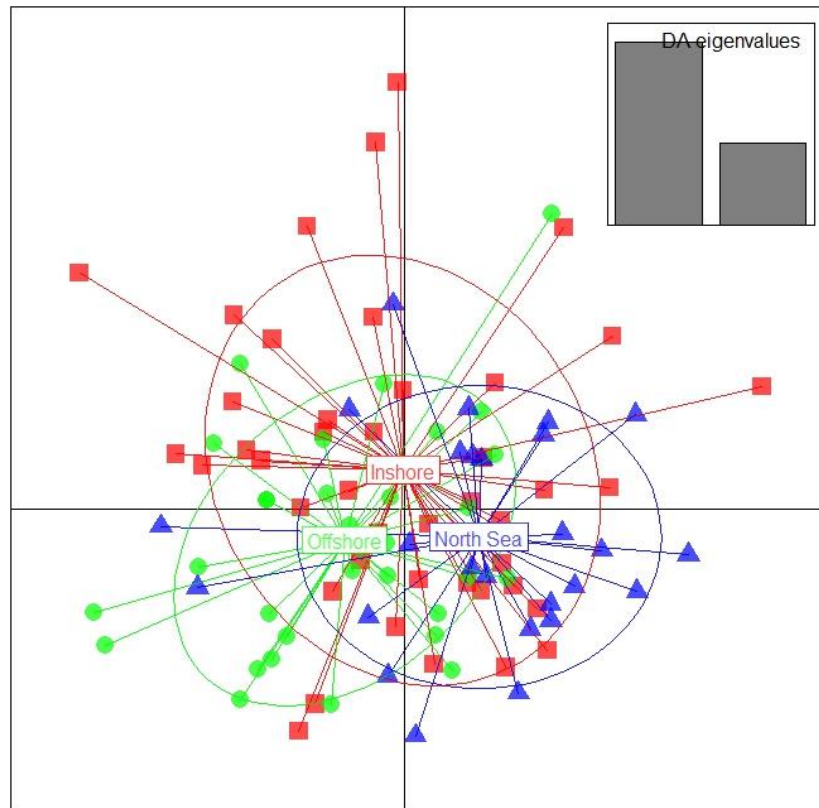


Fig. 4 Ordination plot of *dapc* for the three sea bass population samples. Resulting genetic clusters are shown by different colours and inertia ellipses, and dots represent individuals. The top-right inset shows the eigenvalues of the two principal components in relative magnitude. The largely overlapping plots suggest low levels of population sub-structuring.



Conclusion

The results of this study also suggest that sea bass from inshore Irish waters, from offshore waters in the Celtic Sea and from the North Sea are part of the same panmictic population.

Acknowledgements

The author was supported by the Beaufort Marine Research Award in Fish Population Genetics funded by the Irish Government under the Sea Change Programme and by funding received directly from the Marine Institute. The authors would also like to sincerely acknowledge the assistance Queens University Belfast for undertaking the sample analysis

and to Mike Armstrong and Mary Brown of CEFAS (Centre for Environment, Fisheries and Aquaculture Science) in the procurement of samples from the North Sea.

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